Exploring the experience of episodic memory: The contribution of sensory modalities and mental imagery to vivid reliving

By

Megan Leah Rudrum

100149117

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

Research undertaken in the School of Psychology, University of East Anglia.
January 2021

Exploring the experience of episodic memory: The contribution of sensory modalities and mental imagery to vivid reliving

Abstract

Episodic memory involves a rich, vivid reliving of past events accompanied by a multitude of sensory details. The focus of this thesis was to further understand the processes that support this rich reliving in episodic memory. The study in Chapter 2 used electroencephalography (EEG) to explore differences in neural dynamics between episodic memory replay occurring in multiple modalities (audio and visual simultaneously) or just one modality (audio or visual alone). Results revealed no differences in oscillatory power across the modalities suggesting that oscillatory power may not be sensitive to modality of material for successful replay of event memory. Chapter 3 employed transcranial magnetic stimulation (TMS) to disrupt the functioning of the angular gyrus, and examined performance for recognition and source recollection, as well as confidence, to determine if interrupting multimodal feature integration impacted the subjective experience reflected in confidence of recollection. The data revealed a trend for reduced confidence of multimodal recollection following angular gyrus stimulation compared to a control site. The studies in Chapter 4 turned towards examining how individual differences may impact the experience of reliving, focusing on individuals' ability to use object and spatial imagery to mentally picture sensory information in the mind's eye. Results demonstrate that object imagery ability predicts a sense of reliving both for recent memories and remote memories, while spatial imagery ability is related to subjective judgements about spatially related manipulations. It establishes that imagery ability needs to be measured as separate constructs and considered carefully in regard to what memory process is being assessed. The work conducted in this thesis has contributed to furthering understanding of the neural correlates and individual dynamics that support reliving in episodic memory as a vivid multimodal experience.

Access Condition and Agreement

Each deposit in UEA Digital Repository is protected by copyright and other intellectual property rights, and duplication or sale of all or part of any of the Data Collections is not permitted, except that material may be duplicated by you for your research use or for educational purposes in electronic or print form. You must obtain permission from the copyright holder, usually the author, for any other use. Exceptions only apply where a deposit may be explicitly provided under a stated licence, such as a Creative Commons licence or Open Government licence.

Electronic or print copies may not be offered, whether for sale or otherwise to anyone, unless explicitly stated under a Creative Commons or Open Government license. Unauthorised reproduction, editing or reformatting for resale purposes is explicitly prohibited (except where approved by the copyright holder themselves) and UEA reserves the right to take immediate 'take down' action on behalf of the copyright and/or rights holder if this Access condition of the UEA Digital Repository is breached. Any material in this database has been supplied on the understanding that it is copyright material and that no quotation from the material may be published without proper acknowledgement.

Contents

List of Tables

List of Figures

Acknowledgements

To my supervisor Dr Heidi Bonnici. This thesis would not have been possible without your guidance and your faith in me. You helped me to believe in myself and my abilities. The journey to a completed thesis was more difficult than either one of us could imagine but I will always be grateful you were my supervisor and that we worked together through the bad and the good. The last time we spoke you told me how proud you were following my viva. I will always be glad that you knew I had passed. The world has lost a great scientist with you gone and I will always be enternally thankful I had the priviledge of working with you.

This thesis would not have been possible without the support of a wide network of staff and fellow students across the UEA. A big thank you to my second supervisor Dr. Louis Renoult. Your guidance with my EEG data analysis was invaluable and your positive encouragement always helped see me through. Dr. John Spencer, my third supervisor, I am thankful for the feedback and advice in my review meetings. To the School of Psychology staff old and new, thank you for the continued support. In particular, Jackie Orford, Yvonne Kirkham, Scott Steward-Smith, and Emma Elliott. You all answered my questions, supported my concerns, and were always on hand to help. Additionally, Malcolm Rae and Richard Carey-Knight thank you for your support in getting the TMS equipment and lab running. Further thanks to Gillian Potter from the PGR office who helped guide me through the submission and final processes and to Rosemary Bass at Careers Central for support in growing wider skills.

Thank you to all my family and friends. All your support means the world to me. A particular thanks to my friends. Dr. Kerri Bailey, thank you for being my office buddy and making me smile as we worked through our problems on our coffee breaks. Dr. Rachel Lambert, I cannot thank you enough for being my voice of reason, listening to me, and encouraging me. I truly enjoyed working and teaching together. Dr. Ian Norman, thank you for your words of wisdom and advice which helped me survive the PhD. I am thankful to the three of you for our online coffee morning calls that kept me sane during the pandemic. Dr. Ethan Knights, thank you for your support when I needed you and coming on walks around the lake to escape the office at lunchtime. To my family, I appreciate your understanding and support. A particular thanks to my mum, Michelle Thompson. You are my biggest

cheerleader and helped make me into a strong independent thinker who had the courage to go back to university as a postgraduate. To our cat Nelson, you came to live with us as I started this PhD and saw it to the end providing cuddles whenever needed.

Finally, thank you to my husband Adam Rudrum. Without your love and support this thesis would not have been completed. You have been there for every hurdle and celebrated every success with me. Despite my incessant use of acronyms which you hated, you put up with me brainstorming out loud and my paperwork everywhere. I cannot thank you enough and know that this work would not be possible without you.

Author's declaration

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

Parts of this work has been presented at conferences:

Poster Presentations

Rudrum, M., & Bonnici, H.M. (2018, September). *Decoding unimodal and multimodal episodic memory in EEG*. Poster session presented at the meeting of the British Psychological Society East of England, Norwich, UK.

Rudrum, M., FitzGerald, T.H.B., & Bonnici, H.M. (2019, March). *Decoding power spectra in unimodal and multimodal episodic memory recollection.* Poster session presented at the meeting of the Cognitive Neuroscience Society, San Francisco, USA.

Oral Presentations

Rudrum, M. (2018, November). 3 Minute Thesis Competition. University of East Anglia, Norwich, UK.

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

Name: Megan Rudrum

Signature: M.Rudrum

Date: 11/01/2021

Chapter 1

-

General Introduction

1.1. Prelude and thesis overview

At the heart of this thesis is the aim to further understand the processes supporting reliving and re-experiencing of a past event in rich and vivid detail. Episodic memory is usually accompanied by a rich and vivid sense of reliving involving sensory information, including such as what was seen and heard. This sensory information needs to be supported by integration to ensure a full recreation of an event as a whole entity. Furthermore, an individual must also be capable of vividly recreating the memory experience in the absence of the external event in order to fulfil this sense of reliving. Both integration and mental imagery contribute to the phenomenology (the subjective experience) of reliving.

The main aim of this thesis is to explore the elements of reliving an episodic memory as a rich and vivid experience. I focus on the sensory-perceptual elements of vision and sound, examining when memory is recollected in one modality or integrates multiple modalities, and investigating mechanisms that support event memory. A secondary aim is to establish if there are individual differences in the re-experiencing of memory, focusing on individual differences related to mental imagery ability, as literature suggests that the ability to picture mental images in the mind's eye can vary considerably between people. I look at these aims in 3 ways: I look at the neural patterns that support multimodal and single modality replay of event memory; I examine behavioural responses when a region thought to relate to multimodal integration is disrupted; and I study self-report measures of mental imagery ability, and how this can relate to aspects of memory recollection.

Chapter 1 presents an overview of relevant literature and concepts that are important within episodic memory; the aim being to provide a contextual foundation of the topic and how it relates to the aims of the thesis. In Chapter 2, I examine the oscillatory dynamics, as investigated with electroencephalography (EEG), that support unimodal and multimodal episodic memory; that is, when we remember using one mode as well as integrating across them. In Chapter 3, I investigate the behavioural consequences of disrupting a brain region suggested to support integration of a multimodal event memory. Using transcranial magnetic stimulation (TMS), I target the left angular gyrus to interrupt typical functioning of the region and examine both objective and subjective measures of episodic memory responses to more specifically assess any impact. Chapter 4 addresses the role of mental imagery in episodic memory and how individual differences can influence how we remember. If sensory details contribute to reliving an episodic event then it is vital to understand what impact, if any, an individual's ability to mentally picture details can have on episodic memory. Finally, in Chapter 5, I provide a general discussion of the findings in relation to the aims of the thesis.

1.2. Introduction

The study of memory is fundamentally multi-disciplinary. From philosophers and psychologists, to writers, poets and the lay person, there is a desire in many fields to further understand and explore the idea of 'what is memory?'. (For further reading covering several perspectives see *Memory: An anthology* by Wood & Byatt, 2009). In the following literature review I first outline how the study of human memory has developed in the field of psychology, including the theoretical approaches that have contributed to what we know about memory in cognitive psychology today and models of memory. The focus of this thesis is a specific memory system within these larger models, therefore I go on to establish what is meant by episodic memory, including the relationship of episodic memory to other memory systems and how we can measure this type of memory in particular.

Following the establishment of memory systems and what is meant by episodic memory, the following review focuses on elements related to episodic memory specifically. I look at key brain regions involved in representing episodic memory, highlighting the role of the parietal cortex in qualitative aspects of recollection. I discuss how modalities in memory are not always equal, a key consideration for how we re-experience our past. Finally, I examine the relationship between mental imagery and episodic memory. It is generally agreed that some form of memory representation must occur for the recall of material, and mental imagery has often been linked with episodic and autobiographical memory. I thus review how individual differences in mental imagery can impact memory for previous events.

1.3. Approaches and models of memory

The term 'memory' is an overarching term that encompasses a great many elements. In order to understand where we are with the study of memory today, it is important to first understand how the study of memory has unfolded. The following brief overview of the history of memory is by no means a comprehensive review, rather the aim of this section is to provide context for the area of memory this thesis is focused on and how we have reached the present view of structure within human memory.

A 19th century philosopher and psychologist, Ebbinghaus is thought of as the first person to study memory experimentally. He taught himself nonsense trigrams (three letters) in attempt to remove meaning and latter examined his recall. His work made significant contributions to the study of memory and some of his principles still remain prevalent today, including the learning curve and serial positioning (Ebbinghaus, 1885; also see Murdock, 1985). A key choice in his use of nonsense trigrams rather than words was to deprive the stimuli of meaning, successfully demonstrating that learning and memory can occur without attaching meaning.

In the early 20th century, behaviourism was a prominent approach in experimental psychology. This approach focused on the observable: it examined observable behaviour and responses from environmental stimuli. Due to the concept of 'memory' being unobservable, focus was directed more so at learning as a measurable outcome of exposure to input. Also in the 20th century, Gestalt psychology started to apply principles from the study of perception to memory. This alternative perspective emphasised the presence of internal representations and the role of the individual in remembering. Similar to Gestalt psychology in arguing for the importance of the person remembering, Bartlett proposed that meaning to an individual was indeed important to memory. He suggested that individuals build what he termed 'schemas' or internal representations about how they believe the world around them was structured. New information could be integrated into an existing schema and recalled (Bartlett, 1932; see Carbon, 2012; Wagnoner, 2013).

These three approaches to the study of memory all could arguably account for some stimulus-response outcome of the memory. However, behaviourism was too reductionistic and largely ignored any explanation between stimuli and behaviour. Both Gestalt psychology and Bartlett’s approaches relied on the concept of an internal representation but devising a way to study these internal elements was not possible at this point. By the middle of the 20th century computers were developing, and more information-processing approaches became prevalent. The digital computer and its memory ability provide a nice analogy to human memory: both human memory and a computer system need to be able to have information enter (encoding), a capacity to hold the information (storage), and a facility to find and recall the stored information (retrieval) in order to function (Baddeley, Eysenck & Anderson, 2009).

Accompanying the development of cognitive psychology was the shift from viewing memory as a unitary system towards memory being comprised of several memory systems. The multistore model of memory (also known as modal model) by Atkinson and Shiffrin (1968) proposed stores of sensory memory, short-term memory (STM), and long-term memory (LTM). This model provides a very similar structure to the above computer analogy, and whilst useful in conceptualising there are several memory systems, it is very simplified. Evidence has demonstrated that, within both the STM and LTM stores, there are even more components rather than themselves being unitary systems.

The working model of memory (Baddeley & Hitch, 1974) demonstrates components within STM. This model posits that there are separate stores depending on the modality of input and this is co-ordinated by a central executive component for entry into LTM (see *Figure 1.1*). The phonological loop deals with spoken and written material, formed from two parts termed the phonological loop and the articulatory control process. The visuospatial sketchpad oversees information inputted in a visual or spatial format and allow manipulation of visual information.

Baddeley (2000) later updated the working model by adding a component termed the ‘episodic buffer’. This component serves to provide an interface between LTM and components of the working memory model and allowing representations from separate modalities to be integrated to form one coherent representation. The episodic buffer solves some of the criticisms from the original model regarding how information is bound together (Gathercole, 2008). Of relevance to the aims of this thesis, the parietal cortex, namely the angular gyrus, has been proposed as the site for the episodic buffer (Vilberg & Rugg, 2008; for a recent review of angular gyrus see Humphreys et al., pre-print) which I discuss further in a later section.

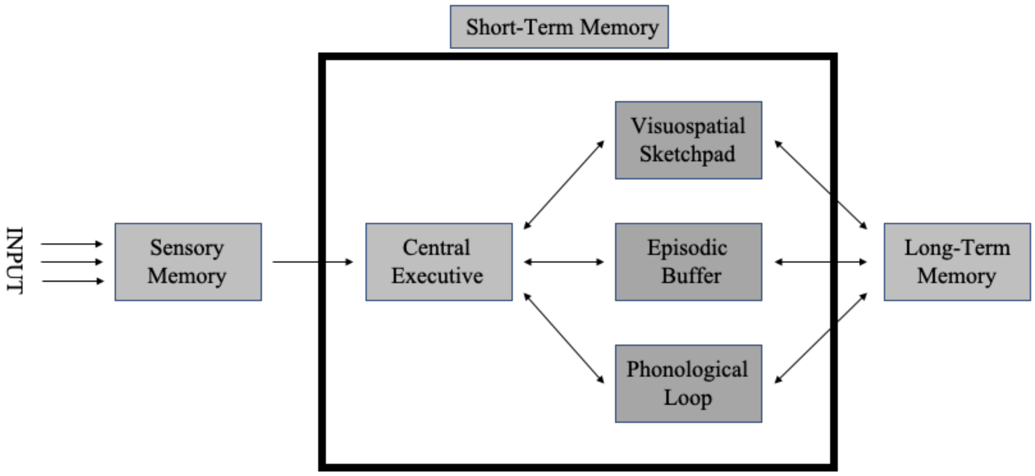

Figure 1.1. Representation of the structure of multistore model of memory and the working model of memory as they may link together. Inspired by the working model of memory (Baddeley & Hitch, 1974; Baddeley, 2000), these components are represented with the black box, within an overview of the multistore model of memory (Atkinson & Shiffrin, 1968).

The long-term memory system is equally oversimplified from the early multistore model of memory. For example, Tulving's (1972) distinction between our memory for past events versus memory for factual knowledge, a distinction covered in the next section. Squire's (1992) classification of long-term memory provides a good reference point for how the LTM system can be approached (see *Figure 1.2*). At a broad level, it can be divided into explicit (declarative) memory and implicit (nondeclarative) memory. Within this, explicit memory can be divided into episodic and semantic systems, related to memory for past events and memory of facts/knowledge respectively. Implicit memory covers skills, priming and unconscious processes, for example, riding a bike. This division of systems accounts for findings in amnesic patients such as Clive Wearing (Wilson & Wearing, 1995) where LTM was impaired for both events and facts but was intact for playing the piano.

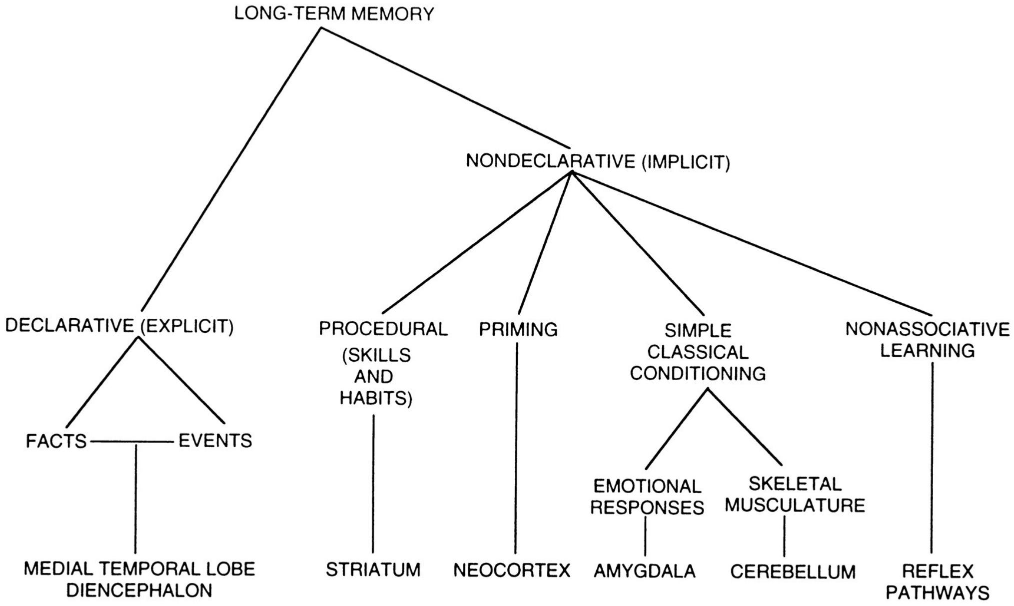

Figure 1.2. Representation of division within long term memory taken from Squire & Zola (1996).

The evolution of approaches to memory has driven the view of human memory as a complex set of systems. It has moved beyond a simple stimulus-response approach to acknowledging internal processes of encoding, storing, and retrieving information. Input can come from various sensory modalities to be processed and the episodic buffer is a proposed unit that integrates these modalities and serves as an interface with long-term memory. Episodic memory is one system within the long-term memory umbrella. Although Squire's (1992) classification is a helpful visualisation of LTM, the divide between episodic (events) and semantic (facts) is likely not as clear cut as this would suggest. It this next section I discuss how episodic memory can be distinguished from other types of memory and ways in which it can be measured.

1.4. Episodic memory

The concept of episodic memory has evolved substantially over the past 50 years. The early distinction between episodic memory and semantic memory proposed by Tulving in 1972 focused on dividing them as personal events verses general knowledge respectively. This basic distinction at its core is helpful in conceptualising a difference, however more precisely what defines the two proposed memory systems is more complex. Since this early work, Tulving has developed and revised his original description of what compromises episodic memory and responded to criticisms (e.g. Tulving, 1983; 1985; 2005), with much of his concepts still highly influential in memory research today (for a recent review of the evolution of Tulving's work, see Renoult & Rugg, 2020).

A key feature of episodic memory is that not only are sensory-perceptual details of a past event recalled, these details are also mentally re-experienced as if the event itself were occurring again (Wheeler, Struss & Tulving, 1997). According to Tulving (1983), episodic memory involves a subjective sense of time (also termed as mental time travel; Tulving, 1985). Unlike a clock or a calendar following a chronologically and measurable 'objective' time, subjective time allows the person remembering to follow a subjective experience of travelling back to the event and reliving in their own concept of time. Comparatively to a physical approach of measuring time, this subjective time is unquantifiable as it is a product of the mind and controlled subjectively by the rememberer. For example, an event that transpired over hours in objective time could be recalled in subjective time in mere minutes.

Linked to the experience of mental time travel is autonoetic consciousness (also termed autonoesis). Autonoetic consciousness is the ability to engage in mental time travel which allows awareness of the self in a subjective time (Tulving, 1985). This is in contrast to noetic consciousness, associated with semantic memory, where there is an awareness of 'knowing' past information such as the name of a friend but there is no sense of self in the past or a recollective experience (Gardiner, 2001).

In a recent review by Renoult et al. (2019), they re-examine the distinction between episodic and semantic memory through similarities of both systems found in neuroimaging, neuropsychological, and behavioural data. The authors conclude that whilst there is considerable overlap between episodic and semantic memory, there remains some distinctiveness in the neural correlates and that task demands along with time has a bearing on the representation. This review highlights that whilst the term episodic memory is useful in describing a type of memory system, it is intrinsically linked with semantic memory and this should be considered when interpreting findings. The present thesis uses the term episodic memory to describe the recollection of events that have context (a unique place and time) and are accompanied by autonoetic awareness that allows the re-experiencing of the event. Critically, it is the ‘recollection’, defined as having context and a feeling of re-experiencing, that characterises episodic memory.

1.4.1. Episodic memory and autobiographical memory.

Closely related to episodic memory is autobiographical memory. When discussing both episodic and autobiographical memory, both involve previously experienced events being retrieved and re-experienced. Given this it is understandable how sometimes the terms are used interchangeably or that autobiographical memory is a special case of episodic memory (e.g. Gardiner, 2001). However, while the two are closely related, there are arguable differences between the two terms and modes of memory.

Indeed, Conway and Pydell-Pearce (2000) and Conway (2001) argue that instead of the episodic-semantic distinction, there should be a third system of the self to encompass the unique aspects of autobiographical memory. For example, Conway (2001) describes the difference of episodic and autobiographical memory by time frame: episodic memory is measured in terms of minutes, hours, whereas autobiographical memory develops on a much longer time scale of weeks, months and years. By this view, an episodic memory that is a highly rich sensory-perceptual experience is added into an autobiographical memory structure over time.

Autobiographical memory can be described as being composed up of several components, including episodic memory, visual imagery, semantic processes, self-reflection, and more (Svoboda et al., 2006). This conceptualisation of autobiographical memory emphasises that this type of memory relies on several systems, including that of episodic memory, but that in order to encapsulate the autobiographical nature around the self it does not necessary need episodic memory. For example, one can have autographical knowledge that they have a brother but can also recall a specific autobiographical event related to that brother’s birthday party. This outline of autobiographical memory highlights a similar view to Conway (2001) in that episodic memory is part of a larger system supporting autobiographical memory along with other components. Further, it demonstrates the need for an integrative mechanism to allow a complete autobiographical remembering experience.

We can also see evidence of the distinction between episodic memory and autobiographical memory in the networks that support the retrieval. Gilboa (2004) conducted a meta-analysis of neuroimaging studies focusing on the activation in the frontal lobes for 14 studies of autobiographical memory and a matched number of episodic memory investigations based on the content they examined. While there were some similarities present in the retrieval systems, some differences were also present in functional activation such as right mid-dorsolateral PFC for episodic but not autobiographical memory, and ventromedial PFC for autobiographical but rarely episodic memory. They propose this demonstrates the two areas are used differently for assessing the different types of memory and highlight functional neuroanatomical evidence for considering them as separate systems. It further suggests that at least some caution should be taken when considering what type of memory is being examined, the timeframe and possible assessment factors such as elaboration that could influence the network being recruited for retrieval.

The examination of personal semantics, the knowledge of one's own past, may bridge the gap between autobiographical memory and semantic memory (see Renoult et al., 2012). Personal semantics can be examined by looking at Autobiographical Significant Concepts (ASC). ASC are semantic concepts strongly associated with specific episodes that have personal significance. For example, having knowledge about the Harry Potter books plus the recollection of reading 'Harry Potter and the Deathly Hallows' last week would be an ASC. This intersection of semantic knowledge and episodic of personal relevanc demonstrates the need for integration across memory systems for a complete experience when we examine our past. Examination of the neural correlates of ASC also support an episodic element to semantic concepts. The late positive component (a neural component associated with episodic memory) was greater for recognition of famous names that had high ASC compared to those with low ASC (Renoult et al., 2014). Overall, it demonstrates that even semantic concepts can have a high relationship to an episodic experience.

While there is a strong relation between the two types of memory, in order to fully understand how human memory works it is important to acknowledge even such subtle distinctions in the way both modes of memory are conceptualised. It has consequences for how we understand and interpret the mechanisms that support different experiences of memory and develop interventions. Here, I refer to episodic memory as a shorter memory system for reliving sensory experiences and acknowledge that autobiographical memory is closely related but should not be used completely synonymously with episodic memory. When discussing autobiographical memory, I refer to memory for prior events from a longer time period that have had a chance to be rehearsed on a greater scale and thereby also built into a personal schema related to the self.

1.4.2. Investigating episodic memory.

There are a variety of ways to test episodic memory and investigate differing aspects of the episodic memory system. In free recall tests participants are asked to remember material previous experienced in any order, whereas serial recall requires the studied materials to be remembered in the order they were presented. In cued recall tests the recall is based off a given cue, such as learning word pairs and then at recall being given or ‘cued’ with a word and recalling the associated word. So called what-where-when tests have also been employed as a way to examine memory for an entire event and encapsulate more elements of an episodic event memory. Alternative to recall tests, recognition judgement tests are also a way to examine episodic memory. Recognition judgement tests require participants to identify previously experienced material that is intermixed with unstudied materials and source judgement tests require identification of the context in which a studied item was learnt, such as if it was present visually or auditorily, or as a word or picture (see Cheke & Clayton, 2013).

Additionally, the phenomenology or the experience of the memory itself can be examined. Phenomenological characteristics such as belief, emotion, perspective, and more can also provide a detailed insight into how a person is reliving a past event. Self-reflection on the memory experience can be accomplished through ratings of confidence judgements such as how accurate a participant believes they are on a recognition decision, or a vividness judgement on how well a participant can picture a past events. Paradigms such as Remember/Know (Tulving, 1985) also examine the feeling associated with the memory as to whether a participant actively recollects the event rather just feeling like the cue is familiarity but does not actual recall the event experience.

A key consideration when looking at tests of episodic memory is if they are truly assessing whether the memory experience is episodic in nature (i.e., a recollection experience; see above). The term episodic memory can refer to the memory system or to the type of test that is examining event memory; a test of episodic memory does necessarily mean that the memory meets our earlier discussion of what makes a memory episodic (see Wheeler, Struss & Tulving, 1997 for discussion of terms). For example, a recall test explores the ‘what’ of memory, but not whether the memory was accompanied by a sense of re-experiencing the context in which the item was learnt. In comparison, source memory judgements are more likely to be assessing the context of the experience as the response requires reflection on the learning experiencing and by extension the memory of the event. Therefore, a memory test that only examines what is recalled does not always equate to measuring a true episodic memory experience. Care must be taking in what can be claimed about the episodic memory system depending on how it is being measured as they are not certainly measuring the same concept.

Advances in neuroscientific techniques has also helped the investigation in episodic memory develop substantially. Behavioural measures of accuracy and reaction time as well as rating scale all provide a reflection of behavioural differences but do not provide much insight into what supports the memory process. Neuroimaging techniques such as fMRI and EEG allow the regions activated in these memory performances to be compared as well as the timing of such responses. In the next section I review the cortical regions that support episodic memory and related theories.

1.4.3. Brain regions involved in episodic memory.

The cognitive process of episodic memory is unlikely to be confined to one location alone in the brain. Instead, the prevailing view acknowledges that episodic memory involves a large network of interconnected regions both for encoding and retrieval. Some areas of the brain have received more attention than others, such as the medial part of the temporal cortex, partly due to early patient observations. The precise contribution across the network is nuanced in that different areas of the network can be recruited depending on task requirement. For example, frontal cortical areas seemed to be involved in strategic aspects of retrieval whereas left parietal regions more so with retrieval success (Buckner & Wheeler, 2001). As to the medial temporal lobe (MTL) regions, and in particular the hippocampus, research suggests that it mediates episodic memory processes of binding together details into a mental representation (Moscovitch, Cabeza, Winocur & Nadel, 2016; Mullally, Vargha-Khadem & Maguire, 2014; Rubin & Umanath, 2015). Sensory cortices also seem to be involved in memory. For example, Wheeler, Petersen and Buckner (2000) found that vivid recall of sound and pictures was associated with activation in sensory cortices also active during perception.

The MTL, in particular the hippocampus and surrounding regions of the parahippocampal, entorhinal, and perirhinal cortices, have long been connected with discussions of the brain regions supporting episodic memory (Rugg & Vilberg, 2013). Of significant note to MTL involvement in episodic memory is the patient study of HM (for a discussion of the contribution of H.M. to neuroscience see Squire, 2009). In experimental surgery to prevent seizures H.M. had parts of his MTL removed that included the hippocampi, amygdalae, and parahippocampal cortices. Following the surgery H.M. suffered from severe anterograde amnesia; he was unable to generate new declarative memories despite other aspects of his cognitive functioning remaining intact. This led to conclusions that MTL was a vital region in the formation and recollection of episodic memories (e.g. Smith & Kosslyn, 2007). Advancements in understanding the role of episodic memory processes have since linked the hippocampus to the reconciliation of details to allow a mental representation (Moscovitch, Cabeza, Winocur & Nadel, 2016; Mullally, Vargha-Khadem & Maguire, 2014; Rubin & Umanath, 2015).

While the hippocampus has a long association with recollection of the past, research also suggests that this is not the primary function but rather one of several cognitive aspects it plays a role in (see Maguire & Mullallay, 2013). The hippocampus is linked to other cognitive functions such as spatial navigation (Spiers & Maguire, 2006). It has also been linked to imagination of events, such as thinking about fictious experiences (Hassabis, Kumaran, Vann & Maguire, 2007) and future thinking (Hassabis et al, 2007; Schacter & Addis, 2009). Note the difference between future thinking and fictious thinking is that only the former is personally relevant and requires self-referencing from current autobiographical knowledge. It suggests that the hippocampus is engaged not just in episodic memory processes but rather in the generation of scenes.

Scene construction theory (Hassabis et al., 2007; Hassabis & Maguire, 2009; Maguire et al., 2016) posits that the role of the hippocampus is to construct spatial elements of mental representations. A spatial context of an experience allows further details to then be built into the representation (Mullally & Maguire, 2013). This account explains how MTL process support mental representations for remembering our past as well as future thinking and fictious thinking using a spatially coherent scene as a foundation. An alternative avenue of work suggests that hippocampal episodic memory processes relate all forms of information together, rather than just spatially relevant information (Eichenbaum, 2016; Olsen, Moses, Riggs & Ryan, 2012).

Both views support the processes of mental representations in MTL processes. Critically the difference between the two viewpoints on the role of episodic memory processes mediated by the hippocampus outlined above is scene versus event representation. Scene-based representations focus on a spatial context with more perceptual specificity, whereas event-based representation includes aspects such as temporal sequence of information (Sheldon & El-Asmar, 2018). It suggests that episodic memory process can contribute to different types of mental representations – one that is scene based and another that is event based.

The parietal lobe is another area of particular interest in the study of episodic memory. Evidence from neuroimaging investigations demonstrate parietal activation in successful retrieval of episodic memory (Rugg & Vilberg, 2013; Wagner et al., 2005; for reviews see Rugg & King, 2018; Sestieri, Shulman & Corbetta, 2017). Yet mixed findings on the precise role of parietal region presents an interesting target for episodic memory investigation. For example, despite regular parietal activation in neuroimaging studies patients with parietal lesions still show accurate performance on some episodic memory task (Simons et al., 2008).

More specifically the angular gyrus within the parietal cortex has attracted a great deal of interest (for a review of angular gyrus function across several cognitive elements see Seghier, 2013). Located in the posterior inferior parietal lobule, the angular gyrus corresponds to Brodman area 39. Additionally, the angular gyrus sits at the convergence of white matter pathways connected to areas associated with sensory processing and episodic memory regions across the frontal, parietal, and temporal lobes (Caspers et al., 2011; Uddin et al., 2010; see all Seghier, 2013 for a summary). There are several theoretical accounts addressing the function of parietal cortex and angular gyrus in memory. Its location at the junction between parietal, occipital, and temporal lobes makes the angular gyrus a good candidate as a hub that integrates information from different subsystems and modalities, and strong connectivity with the hippocampal system (Seghier, 2013). It has been suggested as a suitable convergence zone for information from sensory cortices to be integrated (Binder et al., 2009; Damasio, 1989; Shimamura, 2011). This integration into a singular representation has been extended to memory. The angular gyrus has shown a preference for multimodal recollection over unimodal recollection (Bonnici et al., 2016; Yazar, et al., 2017).

One account proposes the role of the angular gyrus is to act as the "episodic buffer" (Vilberg & Rugg, 2008). The episodic buffer is a component of the multi store model (Baddeley, 2000; see above section for further details of the model) which acts as an interface between modalities and the long-term memory store. An alternative account is that parietal activation reflects an attentional mechanism rather than a memory related mechanism (Cabeza et al., 2008). This theory suggests that the activity demonstrates internal attention being directed towards the memory process.

The subjective experience account proposes that the angular gyrus is central to enable a rich reliving experience typically described in episodic memory (Moscovitch et al., 2016; Simons et al., 2010). The integration at this site binds together perceptually rich information which in turn supports the experience of recollection. We see that when the left angular gyrus is interrupted, there is a reduction in source recollection confidence but not for objective recall (Yazar et al., 2014). The contextual integration model (Ramanan, Piguet & Irish, 2018) similarly argues that while the functional role of angular gyrus is to act as a convergence zone, the mnemonic mechanism it provides for memory is contextual integration. Sensory-perceptual details are bound together to form a rich representation layer. From this the angular gyrus and MTL interact to promote a subjective experience of a vivid recollection, with the angular gyrus contributing the contextual layer. We see evidence of these complementary roles of the hippocampal and parietal regions with enhanced activation in associated areas during retrieval of episodically linked information (Jonker, Dimsdale-Zucker, Ritchey, Clarke & Ranganath, 2018).

More specifically, the multimodal hypothesis posits that it is multimodal integration at the angular gyrus that underpins the subsequent sense of recollection (Bonnici et al., 2016; Kuhl & Chun, 2014). When the angular gryus is prevented from functioning typically, there is a reduction in the number of features recollected from multimodal encoding than if features were presented within the same modality (Yazar et al., 2017). The subjective experience account and the contextual integration model both support the role of integration at the angular gyrus in providing a contextually rich structure to support subjective recollection. The multimodal hypothesis extends this by arguing it is specially the integration of information from multiple sensory modalities that take place within the angular gyrus. It is this multimodal integration that provides the information from which a subjective recollective experience can occur.

In patients with posterior parietal lesions there appears to be disrupted scene construction ability with less sensory-perceptual detail and poor scene generation (Berryhill, Picasso, Arnold, Drowos & Olson, 2010). A similar finding was observed in Alzheimer’s disease patients with greater posterior parietal atrophy (Irish et al., 2015). It suggests a constructive role of parietal cortices and notes the importance of it for sensory details in recollection. However, in these cases an attentional account cannot be ruled out.

A study by Bonnici and colleagues (2016) demonstrated that the angular gyrus showed greater activation for multimodal memory replay compared to replay in a single modality (either auditory or visual). In their fMRI investigation, prior to scanning participants learnt to vividly and accurately mentally replay nine clips: three auditory, three visual, and three a combination of visual and auditory modalities. During scanning they were asked to recall the clips over the learnt 6 second interval and rate how vivid the replay was. Angular gyrus activity was significant greater for the multimodal memory replay compared to either auditory or visual replay alone. Multivoxel pattern analysis could even distinguish between the multimodal memories. Furthermore, the classification accuracy of this tracked with the trial-by-trial vividness reports of recollection. An attentional account alone would not explain why these could be differentiated as it would require the same attentional mechanism for each multimodal memory and therefore not distinguish between the memories. It leaves further questions about the role of the parietal cortex in multimodal memory specifically. For example, if the angular gyrus has a causal role in integrating multimodal representations and by extension a subjective recollection experience.

1.4.4. Episodic memory summary.

A great deal has been established about episodic memory over the past several decades both from a theoretical and from an experimental point of view. Yet there still remains much to be understood about episodic memory retrieval, in particular about the reliving experience especially how it works across different modalities, and whether it varies significantly between individuals. This thesis intends to use the advantages of neurocognitive techniques and behavioural paradigms to understand the mechanisms that support episodic memory for stimuli type across modalities. In particular I focus on the role of the parietal cortex in the qualitative experience of episodic memory when remembering in one modality or multiple modalities.

1.5. The role of sensory modality in episodic memory

If episodic memory is understood as a rich reliving of previously experienced events, then we need to understand how each modality is remembered as well as how memory occurs for multiple sensory modalities. There are two aspects to be considered in regard to modality: the modality of the remembered event, and the modality used at encoding such as a cue in an experiment. In this work I focus on the modality of the memory content rather than the cue used to retrieve the content in order to determine how modality is linked to a rich reliving experience.

The strength of memory across modalities does not appear to be equal. Memory for visual items is generally very good; for example, participants have high recognition accuracy for large numbers of images they have only seen for a short period of time (e.g. Standing, 1973; Brady, Konkle, Alvarez & Oliva, 2008). On the other hand, auditory memory does not appear to have equal performance as that of the visual modality. This can be observed in nonhuman primates where research demonstrates inferior performance on auditory memory compared to visual and tactile (Colombo & D'Amato, 1986; Cohen, Russ & Gifford, 2005; Kojima, 1985) and in human studies (Bigelow & Poremba, 2014; Jensen, 1971). Cohen, Horowitz and Wolfe (2009) compared memory performance in a recognition paradigm for auditory stimuli across a variety of sound types against visual stimuli performance. Accuracy for auditory stimuli could not match that of visual stimuli. Even when sound clips were paired with pictures of objects, there was no improvement in recognition performance for the sound clip alone.

On the other hand, other research has argued that auditory and visual memory are equivalent, but the difference in performance is due to non-equivalent stimuli or variation in tasks. For example, Visscher et al. (2007) looked at performance for visual and auditory stimuli equated for their discriminability using artificial nonverbal sounds. They found that for both stimuli types there was equal performance, suggesting that previous difference may be due to non-equivalence of stimuli. This is in line with Cohen et al's (2009) findings that when visual stimuli were severely degraded performance was equal to that of auditory. However, if the stimuli is degraded then it is not necessarily a fair comparison on the experience of memory in typical situations.

Bigelow and Poremba (2014) looked at performance across auditory, visual and tactile modalities. Auditory performance was worse than visual and tactile at longer retention times. Additionally, they created complex naturalistic multimodal stimuli at encoding and tested recognition. Recognition for audio information following a delay period still remained poorer, but all modalities were equal at identification. It suggests that time from encoding is an important consideration when examining modality and reliving a past experiences.

The focus of this thesis is rich re-experiencing of past events and the modality of that re-experiencing. However, it is also important to note that the modality of input is also of importance. If we consider the basic overview of the multistore model (see *Figure 1.1.*), then sensory input has to occur in order to progress any further in the memory system. Further, attentional resources have to be allocated across modalities at input in order to process the external environment. There is some debate in this multisensory literature as to whether there are separate attentional resources for each modality or if there is one pool that is shared across (for a review, see Wahn & Konig, 2017). Therefore, it is important to consider that any memory difference seen at recollection may be related to differences at encoding. Moreover, the current review does not focus on the relationship between attentional processes and multisensory integration (the interested reader can refer to Navarra, Alsius, Soto-Faraco & Spence, 2010; Talsma, 2015; Talsma, Senkowski, Soto-Faraco & Woldorff, 2010; Tang, Wu & Shen, 2016). While this is important to consider in the context of reliving, it does not diminish that a full recollective experience includes multiple senses which is the focus of this current work.

In sum visual memory appears to be the most dominant modality in episodic memory. Understanding how stored auditory and visual information are integrated into a whole representation is important to determine how we experience a sense of reliving when we remember our past. Combined with the research on the role of left angular gyrus on integration for modalities, it presents an interesting area for further exploration. For example, what are the consequences of disrupting modal integration from being incorporated into a representation?

1.6. Mental imagery and memory

Mental imagery can be described as a representation and accompanying experience of sensory information in the absence of the external stimuli (Kosslyn, Ganis & Thompson, 2001; Pearson, Naselarus, Holmes & Kosslyn, 2015). This imagery is based on stored information, simulating the experience as if one was almost reliving. Mental imagery can also be referred to as “seeing in the mind’s eye” and involve multiple modes of sensory information (Kosslyn, Ganis & Thompson, 2001; Kosslyn, Thompson & Ganis, 2006). It appears there is a link between visual imagery abilities and the experience of a sense of reliving in memory (e.g. Greenberg & Knowleton, 2014; Irish, Lawlor, O’Mara & Coen, 2011; Rubin, Schrauf & Greenberg, 2003). For example, Greenberg and Knowlton (2014) report that individuals who do not report the use of imagery also report a reduced sense of reliving when reflecting on past events.

Contrary to early behaviourist views, it is now an acceptable assertion that it is possible to mentally depict information. This in turn has implications for episodic memory processes, for example scene construction; it is important to further understand what impact imagery ability has on recollection. Although not a new completely new phenomenon, a condition termed 'aphantasia', characterised by a lack of mental imagery ability, has received renewed interest (see Zeman et al., 2015; Keogh & Pearson, 2017). After Zeman et al.'s (2015) work was published, it led to wider acknowledgement beyond psychology that mental imagery may not exist in every individual, and an individual may not even realise they do not use mental imagery (e.g. Clemens, 2018; Lawrence, 2020). Additionally, those who report having aphantasia also report a reduction in imagery in other senses beyond visual imagery (Dawes et al., 2020). Rising evidence emphasises the use of imagery can vary between individuals as well as imagery itself being more than a unitary construct. In the following section I cover the background of mental imagery and then individual differences in imagery.

1.6.1. Brief history of imagery.

As far back as the late 19th century and into the start of the 20th, the connection between visual imagery and memory was considered along with the recognition that the ability to have these mental images varied. Mental imagery was not just left to the realms of philosophers but also had a role in classic experimental psychology. Wilhelm Wundt (1912) proposed there was no difference between the role of perception and mental images on ideas. In his 1890 book, William James highlights a case whereby a friend "knows" what his breakfast table looks like but cannot conjure a mental image of the table itself. He also discusses an example of a person who, while being deaf-mute, still writes about their vivid recollection of scenes. This particular discussion by James is in regard to the nature of thought, but the principles of imagery still apply to other cognitive domains such as memory.

Francis Galton (1880) also observed these differing degrees of vividness between people when remembering.

William James also considered that there might be more than one type of representation: mental images and verbal representations. This idea would resurface around 70 years later in the form of the dual coding theory (see Paivio, 1971). Yet between these times, relatively little progress was made in furthering knowledge about visual imagery. One reason for this is, arguably, a result of the theoretical implications that arose from the advent of behaviourism. This era focused on the observable behaviour, such as reaction times and measurable cause and effect. The element of “the mind” and the possibility that mental imagery was a way to represent information in the mind was considered inaccurate and was simply being confused with inner speech (Pearson & Kosslyn, 2015).

There are also practical challenges to consider in the investigation of mental imagery. Because of the subjective and internal nature of mental imagery, it puts some methodological limitations on the manner to studying. By the 1970’s, new techniques led to the renewal of studying the role of mental imagery in cognition (Kosslyn, 1994). As methodological advances have been made, it has meant that objective measures of mechanisms and neural substrates of visual imagery have been identified (e.g. see Farah, 1989, for a review). The recognition of the role of visual imagery in cognition and mental health, and its ties to perception have helped overcome the so-called imagery debate and establish that knowledge can be depicted in the mind (see Pearson & Kosslyn, 2015, for a discussion).

Both these theoretical and practical aspects have contributed to the comparatively little research in the area of imagery compared to other domains of vision such as visual attention or visual working memory (Pearson, 2014). Moving past the imagery debate and accepting that one can mentally depict information leads to a whole avenue of interesting areas for further research. For example, we now see in the literature investigations into how visual imagery can impact athletic performance and recovery (Driediger, Hall & Callow, 2006). This raises interesting questions such as why there may be variations in imagery ability and what possible consequences could they have (Pearson & Kosslyn, 2015). Here, I am interested in visual mental imagery and its role in episodic memory, in particular if individual differences in this ability to mentally depict scenes have consequences on the way we remember past events.

1.6.2. Individual differences, imagery, and memory.

The history of mental imagery gives rise to several ways mental imagery can be conceptualised: as a phenomenological experience, as a mnemonic device, or as a mental representation. Yet all these concepts are also interlinked and hard to unpick. For example, in order to remember details of a past event, you may create a mental representation to aid your memory and in turn have the experience of reliving. Consideration of all of these factors is important for determining how mental imagery is understood in regard to memory and individual ability. For instance, if one does not have the ability to create a mental representation, does that impact the way they re-experience an event from their past?

Individual differences exist in the way we are able to re-experience our past. In a disorder termed Severely Deficient Autobiographical Memory (SDAM), healthy adults with otherwise intact cognitive function report an inability to vividly recollect their past (Palombo et al., 2015). Examining neurological and behavioural outcomes of 3 healthy adults with SDAM, Palombo and colleagues (2015) found evidence of impaired episodic retrieval for visual information and an absence of typical neural patterns of activity during episodic recollection. However, as long as a task could be completed without episodic processes, their performance was equivalent to other adults. The key difference was the inability to have the recollective experience, something which is considered key to episodic memory.

Conversely, other work has demonstrated the presence of individuals with highly superior autobiographical memory (HSAM; Leport et al., 2012). These two ends of the spectrum suggest that the ability to have a recollective experience, something which we define episodic, may not be a universal mechanism but subject to significant individual differences. The study of the SDAM cases did not allow to discriminate if the deficit in recollection was due to a failure to relate visual details of the event at encoding or to link visual information to cues at retrieval (Palombo et al., 2015). The authors could also not determine if the deficit was secondary for example to an impairment of another mechanism, such as that of imagery.

Vividness of mental imagery as a measure of re-experiencing and its relationship to episodic memory presents an interesting area to examine due to mixed findings. Vividness is a good indicator that sensory-perceptual details of a generated scenario have been engaged with and relived (Wheeler, Petersen & Buckner, 2000). D'Argembeau and Van der Linden (2006) used the Vividness of Visual Imagery Questionnaire (VVIQ; Marks, 1973) to determine if individual variation in producing vivid mental representations had an impact on phenomenological properties of past autobiographical memory and imagined future events. They found that those with richer visual imagery ability reported greater visual details, as well as more detail from other sensory modalities, and a clearer representation of time and spatial information. Yet Greenberg and Knowlton (2014) did not find that vividness ability was a significant predictor of phenomenological properties including sensory-perceptual details. One possible explanation of this conflict can be found in how mental imagery is treated as an undifferentiated construct (Aydin, 2018; Sheldon et al., 2016).

There is evidence that imagery is not a unitary construct (Kosslyn et al., 2001; Thompson, Slotnik, Burrage & Kosslyn, 2009) and imagery ability can be thought of in terms of object and spatial imagery ability (Blajenkova et al., 2006). Spatial imagery ability is, as the name would suggest, referring to the ability to imagine spatial relations between items. Object imagery ability on the hand refers to imagining rich perceptual details. For example, forming a mental representation of your kitchen would likely require spatial imagery to construct the layout of the sink relative to the cooker. Focusing on a specific feature within the kitchen such as the colour of the kettle would utilise object imagery to recreate perceptual features. This distinction appears to hold at a functional level (Farah, Hammond, Levine & Calvanio 1988; Kosslyn, 1994; Logie, 2003), and at a neural level (Kosslyn, Ganis & Thompson, 2001; Mazard, Tzourio-Maxoyer, Crivello, Mazoyer & Mellet, 2004).

The distinction between object and spatial imagery, as well as the range across these two constructs, appears to have varying impacts depending on the memory task being carried out. For instance, disrupting recall using dynamic visual noise appeared to only be detrimental to those with high spatial imagery ability but did not cause a change in performance for self-reports of low spatial imagery ability (Sheldon et al., 2016). Object imagery ability has been correlated with vividness ratings for generating event (‘activities’) and scene (‘place’) representations, whereas spatial imagery revealed no correlation with vividness rating (Sheldon & El-Asmar, 2018). Object imagery has also been linked to higher levels of sensory and perceptual event detail (Vannucci et al., 2016). It suggests that not only does imagery contribute to the experience of mental representation, but that the two aspects contribute in differing manners and depending on ability level.

There seems to be a relationship between a sense of reliving and visual imagery (Greenberg & Knowlton, 2014; Rubin, Burt & Fifield, 2003; Rubin, Schrauf & Greenberg, 2003). Visual imagery is also important for forming mental representations for both past and future events (Greenberg & Rubin, 2003). If we consider theories of episodic memory such as scene construction discussed earlier, then a key aspect is internal representation and constructing spatial and perceptual aspects. A key area of interest then is whether mental imagery ability is a critical and necessary component for episodic memory and in order to produce a sense of reliving. Alternatively, it could simply be one possible component that could be used but is not essential. More work is needed to examine the contribution of imagery to episodic memory processes.

1.7. Current work

The principal goal of this thesis is to expand existing knowledge about the experience of remembering. Episodic memory has a complex history with outstanding areas of interest to allow us to fully comprehend the experience of reliving a memory. To this end, I explore the neural patterns that support recollection in one modality and multiple modalities this time using EEG (Chapter 2).

The parietal cortex, specifically the angular gyrus, is a subject of interest in the memory literature. It has been associated with the representation and integration of sensory information in episodic memory. Additionally, the angular gyrus seems to have an important role in the subjective aspects of memory experience. It is therefore important to know more precisely how it contributes to the experience of memory across modalities. I examine the behavioural consequences of disrupting the angular gyrus in a recognition and source memory task involving unimodal and multimodal stimuli (Chapter 3).

Mental imagery has been connected to forming mental representations and linked to a reduced sense of reliving in episodic memory. Growing literature highlights how individual differences in imagery ability can relate to how episodic memory is used and experienced. I examine how spatial and object imagery ability contributes to autobiographical episodic memory for recent and remote events, as well as specificity of details. Additionally, I examine the relationship between imagery and memory performance on a scene manipulation task (Chapter 4).

Chapter 2

-

Oscillatory dynamics of unimodal and multimodal episodic memory recollection

2.1. Introduction

The recall of episodic memories is usually accompanied by rich and vivid details. This experience is not limited to just the visual domain; information recall comes from various senses that combine to form a complete recollection experience. Multimodal information (also sometimes referred to as multisensory, but for consistency in this work we use the term multimodal) can be defined as information from separate sensory modalities combined to form a single multimodal representation (Stein et al., 2010). Our recall of events usually assesses dynamic situations involving multiple modalities, yet much research explores each mode in isolation (Quak, London & Talsma, 2015). Establishing mechanisms involved in integration of modal information in memory is a critical step in understanding how we can vividly relive the past, something of great importance in relation to age-related memory decline and disorders.

Various types of memory are supported by different anatomical regions of the brain that must work together for cognition. While these regions are often specialised for a certain mnemonic purpose, similar neural oscillations can be found across these regions thought to allow inter-regional communication (Fries, 2005). Examination of oscillations allows further understanding for changes in brain network; we can see how the collective behaviour of neurons is reflected in waves, or rhythmic oscillations (Buzsáki, 2002). Brain oscillations have been proposed as a vital mechanism for storage and retrieval of long-term memories (Fell & Axmacher, 2011; Nyhus & Curran, 2010). In particular, oscillations in the gamma band have been linked with context and feature binding (e.g., Morgan et al., 2011). Theta power has also been correlated with recollective states in memory (e.g., Guderian & Duzel, 2005; Strunk et al., 2017). Understanding the oscillatory dynamics of episodic memory across modalities may provide an insight into what supports integration of sensory information into a unified representation for recollection.

The aim of this chapter is to explore the power of oscillations in the replay of rehearsed memories in either one modality or multiple modalities for all frequency bands. Using the same episodic memory task as Bonnici et al. (2016), the EEG activity of replay in auditory, visual, and multimodal (audio plus visual) modalities was recorded. The power in theta, alpha, beta, and gamma frequency bands were compared to determine the role of oscillations in episodic replay across modalities.

2.1.1. Multimodal integration.

The presentation of auditory and visual information simultaneously can both strengthen and interfere with memory (Shams & Seitz, 2008). In cases where the meaning of the 2 stimuli is related, cueing in one modality can facilitate memory is another (Matusz et al., 2015). Even when meaning of the stimuli may not be perfectly matched in both domains, memory performance for audiovisual is improved compared to unimodal (Cohen & Parra, 2016). It suggests that particularly for auditory and visual modalities, there is a benefit of multimodal information for memory performance. On the other hand, attentional accounts propose that multiple sensory information can distract from sufficient encoding and subsequent retrieval (Craik, Govoni, Naveh-Benhamin & Anderson, 1996).

Despite this disparity, our everyday perception involves multiple modalities of input which could possibly be recollected. A key feature of episodic memory is the coherent representation of a past event, including sensory features such as what was seen and heard. In order to produce a coherent representation, the information from sensory modalities must be bound together. Parietal regions have been linked to the integration of sensory information to form a complete representation. The angular gyrus, located at the junction between parietal, occipital, and temporal lobes, has been proposed as a possible site for sensory integration due to its convenient location and strong connectivity with other systems (Binder et al., 2009; Seghier, 2013; Shimamura, 2011).

Neuroimaging work supports that the left angular gyrus is related to multimodal integration in memory recollection. In an fMRI investigation, Bonnici, Richter, Yazar and Simons (2016) examined the activity of the angular gyrus when mentally replaying a video clip that was either unimodal (visual or auditory alone) or multimodal (visual and auditory features together). They found greater activation in the left angular gyrus during multimodal replay compared to either unimodal condition. Further, multivariate pattern analysis showed that the angular gyrus was able to distinguish between the three multimodal video clips learnt which tracked with self-reported vividness of each trial.

One suggested purpose of the multimodal integration within the angular gyrus is to contribute to a sense of reliving within episodic memory. The finding by Bonnici et al. (2016) that pattern analysis was linked to trial vividness ratings suggest the information within the angular gyrus is linked to the vivid multimodal episodic memory of an event. Neuropsychology findings in patients with parietal damage demonstrate accurate recognition memory but an impaired sense of reliving (Berryhill et al., 2007; Simons et al., 2010). Moreover, these studies report that patients experience less sensory-perceptual details during recall (Berryhill et al., 2007). A similar pattern can be found in Alzheimer's patients with posterior parietal atrophy (Irish et al., 2015). Taken together it demonstrates a possible link between qualitative aspects of episodic memory and multimodal integration.

Whilst fMRI can highlight what brain regions are related to integration of sensory modalities, it cannot provide a complete picture of what neural correlates are occurring in order to support the replay of unimodal and multimodal episodic memory. Examining neural oscillations that support the process through EEG is the next step in providing the full picture of what supports re-experiencing our past as a multimodal, coherent and vivid experience. In the next section I outline what the study of oscillations can add and their importance.

2.1.2. Overview of oscillations.

The study of brain electrophysiology, and oscillations in particular, was a fairly unappreciated area in psychology until more recently. The evolution of psychology over the 20th century and the focus on the observable meant that the 'mind' was overlooked for a period of time (see general introduction). Despite early demonstrations that the brain could be stimulated by electrical current (e.g. the motor cortex by Fritsch & Hitzig 1870), brain electrophysiology was ignored in both psychology and neuroscience until a move towards cognitive psychology mid-20th century (for a review see Karakaş & Barry, 2017). EEG was acknowledged as a scientific phenomenon in 1937 and oscillations have been a phenomenon of interest since, although to a degree of variability, with a particular resurgence in the past 30 years (Karakaş & Barry, 2017).

Today oscillations are an acceptable conceptual and analytical tool in cognitive psychology. EEG offers a non-invasive method to examine neural activation by recording scalp electrical activity. Neural oscillations correspond to rhythmic fluctuations in local field potentials and EEG offers one method of recording this (Thut, Miniussi & Gross, 2012). However, it is worth noting some disagreement about what oscillations actually show. There is some debate as to whether neural oscillations play a causal role in cognitive functioning or whether they are only a secondary effect of the cognitive functioning itself (for a review see Hermann, Strüber, Helrich & Engel, 2016). However, a growing body of literature is demonstrating that brain rhythms are causally linked to cognition (e.g., Thut & Miniussi, 2009; Thut et al., 2012) supporting the importance of understanding oscillations for cognition. One proposed role of neural oscillations is as a mechanism to support brain function both temporally and spatially (Varela et al., 2001); synchronisation of oscillations allows communication between different brain regions (Fries, 2005).

Oscillations can be discussed by their frequency, power, and phase, all of which can be extracted via time-frequency decomposition methods. Frequency can be divided into several bands, including delta (2-4 Hz), theta (4-8 Hz), alpha (9-12 Hz), beta (15-30 Hz), and gamma (>30 Hz). It is worth noting that the precise boundaries of frequency bands vary slightly (Cohen, 2014). Measured in Hertz, frequency is the speed of the oscillation. Power refers to amplitude squared and is a measure of the amount of energy within a frequency band. Phase refers to the position along the sine wave at a given point in time and measured in radians or degrees.

Oscillations establish functional interplay of regions by co-ordinating the timing of neuronal firing through a network (Klimesch, Freunberger, Sauseng & Gruber, 2008). The term ‘neural synchronisation’ is often used when describing oscillations. It is important to clarify our terminology as the meaning of synchronisation can change depending on what is being examined. For example, in animal studies extracellular recording is possible therefore synchronisation refers to correlating spikes and local field potentials in the same or different regions (Fell &

Axmacher, 2011). In human studies, power synchronisation generally refers to an increase (and decrease for desynchronization) in power changes of neurons within a localised region of the cortex as a response to a stimulus (Fell & Axmacher, 2011; Pfurtscheller & Neuper, 1997; Steriade & Llinás, 1988). Note this can also be termed event-related synchronisation and event-related desynchronization (ERS/ERD; Pfurtscheller & Aranibar, 1977; Pfurtscheller & Lopes da Silva, 1999). In contrast, phase synchronisation and desynchronization are independent of the neural firing and reflects the relationship between phase position in two different brain regions.

Power and phase represent mostly distinct neural dynamics, apart from at a very small spatial level. Power is a representation of local synchronisation of neuron potential therefore it is not possible to discrimination power effects and phase synchronisation at a very small scale (Fell & Axmacher, 2011). Both provide valuable information about brain mechanisms for cognition and memory. The focus of the present study is power therefore the following section discusses relevant research to oscillatory power in memory research. That being said, phase is important to acknowledge and has a key role in its own right for memory research. This is not a reflection of diminished importance, only an indication of the scope of the present investigation.

Oscillations provide an advantage over studies of event related potentials (ERPs). ERPs reflect the summative of power across all frequencies locked in at point in time across all trials, whereas oscillations are a reflection of synchronised fluctuations both locally and across cell assemblies (Makeig, Debener, Onton & Delorme, 2004). In sum, exploring oscillatory during memory replay adds a further element to our understanding of neural mechanisms supporting episodic memory. Understanding differences in oscillatory power for episodic replay in varying modalities will help to determine what supports a multimodal recollective experience.

2.1.3. Oscillation power in memory.

Effects of ERS and ERD in power have been demonstrated in several frequency bands, suggesting there is not one specific oscillation associated with memory (Klimesch et al., 2008). This conundrum of the presence of both increases and decreases in power across frequency bands has led to questions over the ‘signature’ of memory formation and retrieval (Hanslmayr & Staudigl, 2014). One suggestion is that synchronisation and desynchronisation that occurs in various frequency bands reflect different processes that support memory function. Hippocampal theta/gamma synchronisation is important for binding episodic information, whereas desynchronisation in lower frequencies (i.e., alpha and beta) is required to represent information (Hanslmayr, Staresina & Bowman, 2016). This framework emphasises a distinction between a hippocampal and neocortical system that work in tandem for their respective responsibilities. One outstanding aspect of the work on oscillatory dynamics is the impact of modality on the replay of episodic memories.

2.1.3.1. Theta.

The theta oscillation frequency band has an established role in both encoding and retrieval of episodic memory (for reviews see Klimesch, 1996, 1997, 1999; Kahana et al., 2001). For example, the extent of theta at encoding can predict memory performance at retrieval (Klimesch et al., 1994). A combination of animal and human research suggests that theta oscillations reflect interaction between the hippocampus and the cortex for episodic memory (for a review see Nyhus & Curran, 2010). Research has also found greater theta at left parietal sites in relation to how well items were remembered (Jacobs et al., 2006). This is a particular area of interest for the present work due to the relationship between parietal regions in integration of modality and the subjective re-experiencing of episodic recollection. Clarification of the precise role of theta also has possible implications for therapeutic interventions in particular for age-related memory disorders (Berens & Horner, 2017).

A large body of work has demonstrated greater theta power for remembered items compared to forgotten items, as well as remembered items compared to new items (e.g. Addante et al., 2011; Guderian & Duzel, 2005; Klimesch et al., 2006; for a review see Nyhus & Curran, 2010). Furthermore, theta power seems to reflect successful recollection, rather than simply item recognition. For example, Guderian and Duzel (2005) found greater fronto-temporal theta power increases when participants made correct context judgements regarding the background faces had been learnt against. This was in comparison to incorrect source judgements and correct rejection of unstudied faces. Strunk et al. (2017) demonstrated similar findings in younger adults, finding theta increase for correct context judgment compared to correct rejections in a similar time range (400 – 800ms).

Theta power has also been studied in regard to other memory related processes including short-term memory and sustained attention. Increasing short-term memory load also increases theta power (Gevins & Smith, 2000; Klimesch et al., 1999; although also see Rondina et al., 2015). Active maintenance of information held in working memory can be linked to sustained theta power increase (Klimesch, Freunberg, Sauseng & Gruber, 2008). The topography of theta power activity can assist distinguishing the possible role of theta in these memory related processes. Theta response can be found in parietal regions for encoding and retrieval of a memory trace, whereas information maintenance and attentional control seems to be associated with sustained theta more so at frontal sites (Klimesch, Freunberg, Sauseng & Gruber, 2008). Jacobs, Hwang, Curran and Kahana (2005) found theta power at left parietal sites correlated with recognition, whereas theta power at central sites correlated with decision making, and widespread theta related to memory load.

There is also variation in the degree of theta power depending on the task. Research shows power varies as an amount of information retrieved for a long-term memory representation, but not due the nature of stimulus (Khader & Rosler, 2011). This leads to the supposition that theta reflects domain general memory operations (Hanslmayr, Staudigl, Aslan & Baunl, 2010; Staudigl, Hanslmayr & Bauml, 2010). However, to the best of my knowledge this has not been assessed when varying the modality of the stimuli. Overall, evidence for the role of theta in episodic memory generally points to top-down retrieval-related control processes (Khader & Rosler, 2011). Further work needs to address if this process is sensitive to modality of the episodic memory recollection.

2.1.3.2. Gamma.

Within the gamma band, increases in power have been associated with a variety of functions, some of which could be necessary to support memory related tasks. For example, evoked gamma has been suggested as a reflection of a matching mechanism to enable stimulus information to be linked to representations stored in long term memory (Hermann et al., 2004). Induced gamma power increases have been found in studies of short-term memory (e.g. Tallon-Baudry et al., 1998), and object representation (e.g. Tallon-Baudry & Bertrand, 1999) among other functions. Additionally, research has shown greater gamma power at parietal sites for remembered items (Burgess & Ali, 2002). One suggestion is that gamma ERS is a reflection of cell assembly activation that is associated with accessing or forming memory traces (Gruber & Müller, 2006).

Recognition memory can be divided into two states referred to as ‘remember’ and ‘know’. The distinction between these two states is that ‘know’ reflects an awareness that you are familiar with the information, whereas ‘remember’ is an indication of retrieving the context of the source of that information and experiencing recollection. Burgess and Ali (2002) examined gamma band activity, comparing recollection versus familiarity of a retrieved memory. They found that recollection induced greater gamma power compared to familiarity. Differences in the two states were localised around frontal (F3, Fz, F4) and parietal (P3, Pz, P4) electrode sites between 30 – 50 Hz gamma range. Furthermore, they found recollection was associated with greater functional connectivity between frontal and parietal regions compared to familiarity. They suggest their work supports a possible association of gamma activity and feature binding (Damasio, 1989; Morgan et al., 2011; Varela, 1995) due to the greater power being observed in a richer memory state. By examining the subjective experience of recognition memory, they were able to compare a contextually rich memory state and against one that was behavioural accurate at recognition but not accompanied by context. It suggests that gamma power increases may be sensitive to the state of subjective experience and perhaps level of detail that support a feeling of ‘remembering’ compared to ‘knowing’.

Gamma power at parietal cortices has been suggested as important for cognitive coordination. Morgan et al. (2011) looked at feature integration in working memory using coloured semi-circles, manipulating visual-spatial properties of colour and orientation. They found greater parietal gamma activity occurred during manipulation of visual-spatial coordinates compared to when manipulating only a single feature. However, more work needs to be conducted to see if this coordination of parietal gamma ERS can be expanded beyond perceptual features of colour and angle in working memory.

Although gamma power increases have been correlated with successful encoding (Long et al., 2014) and retrieval (Burke et al., 2014) in hippocampal recordings from epileptic patients, the precise role of gamma is still unclear. There is some debate over this finding as the power increase likely reflects broadband power, possibly reflecting spiking activity rather than true oscillatory activity (see Hanslmayr, Staresina & Bowman, 2016) and may arise from asynchronous activity (Guyon et al., 2020). Other work has also demonstrated a reduction in gamma power from intercranial EEG (iEEG). Zhang et al. (2015) demonstrated a reduction in gamma power when patients were able to successfully retrace a learnt virtual path. Using representation similarity analysis (RSA), they found higher RSA related to a reduction in gamma power. They argue that this reduction in gamma power is suggestive of an inhibitory mechanism to allow the successful recreation of representations. However, their study looked at similarity of encoding and retrieval, comparing similarity and associated changes in oscillatory dynamics which may not unravel the complete picture of gamma band activity for a wider variety of memory related tasks.

Overall, converging evidence from rodent and human studies across a number of paradigms do support the role of gamma band synchronisation for successful episodic memory (see Hanslmayr, Staresina & Bowman, 2016). The gamma band power seems to have a strong relationship with phase of the theta band. This theta phase and gamma power coupling has been linked to successful episodic memory (Lega et al., 2016). It suggests that gamma power synchronisation is important for episodic memory and is regulated by theta phase, and thereby mediates binding of context (Hanslmayr, Staresina & Bowman, 2016; Staudigl & Hanslmayr, 2013).

2.1.3.3. Alpha and beta.

In contrast to theta and gamma bands, the opposite directionality of power can be found for alpha and beta frequency bands. Both alpha and beta have been linked with desynchronisation of neural firing following a stimulus for successful memory retrieval, as reflected in a reduction of power (for a review see Hanslmayr, Staudigl & Fellner, 2012). I combine the work on alpha and beta bands as the responses in both seem to be correlated. The desynchronisation of alpha and beta have been linked to richness of representation in the brain (Hanslmayr, Staudigl & Fellner, 2012) and may indicate material specific memory reactivation (Hanslmayr, Staresina & Bowman, 2016; Khader & Rosler, 2011; Waldhauser, Johansson & Hanslmayr, 2012).

The topography of the alpha/beta desynchronisation varies depending on material type which has been taken as evidence of content representation. For example, Burgess & Gruzeiler (2000) found lateralisation effects of desynchronisation when comparing retrieval of words and faces. In upper alpha there was less power at temporo-parietal sites left lateralised for words and right lateralised for faces; this effect was reversed in low alpha. Upper alpha and lower alpha were defined based on individual participants due to evidence that memory related differences in the upper and lower range is more apparent when individually determine (Klimesch et al., 1992). In comparison of spatial locations versus objects, have also demonstrated ERD of alpha was maximal at parietal sites for locations and broader for object recall extending over frontal, parietal and temporal sites (Khader & Rosler, 2011). These results have been taken as evidence of material specific representations, likely reflecting the pattern of activity at encoding (Hanslmayr, Staresina & Bowman, 2016). In the present study we aim to determine if this desynchronisation varies across sensory modalities during memory recollection.

2.1.4. The present study.

The aim of the present investigation was to explore the electrophysiological correlates of memory replay in unimodal and multimodal form. In this investigation I used the same task of episodic memory replay as in Bonnici et al. (2016) and recorded the neural correlates via EEG. I focus on oscillatory power for an extended recollection period to examine how an episodic memory can be relived over an extended period of time as one would recall a real event from the past. I look at the average changes in amplitude in the EEG spectrum as a function of time relative to each event condition of audio, visual, and multimodal replay. I compare the changes of one mode (visual or auditory) to multimodal (audio and visual combine) to examine what supports recollection and a vivid and multimodal experience.

Theta oscillations have been linked with top-down control processes in episodic memory and successful recollection. The integration of both audio and visual information into a representation for successful recollection may require more information to be retrieved, which has been linked to an increase in power. Therefore, I predicted greater theta power for the multimodal replay when compared to both unimodal conditions. Gamma seems to have a role in context binding for episodic memory although it is not clear if this is sensitive to modality. If parietal gamma is important for cognitive coordination including that of modality, then I predicted there would be an increase in parietal gamma for multimodal recollection compared with unimodal recollection due to the increased need for integration. In regard to alpha and beta frequencies, the desynchronisation within these bands has been suggested to be content specific and link to richness of a representation. Therefore, I expected there to be a difference in the topography of a decrease in power across sensory modalities.

An additional aim of this chapter was to address if there was a relationship between the phenomenological experience of memory replay and imagery ability. This investigation is interested in the replay of as a recollection experience yet the implicit assumption here is that everyone is able to mentally replay an event. Aphantasia, a mental condition defined by an ability to produce visual mental imagery in the mind’s eye, has been linked to a reduced sense of reliving in memory recall (Zeman et al., 2015; Greenberg & Knowlton, 2014). Additionally, other modalities also appear to be reduced in cases of aphantasia (Dawes et al., 2020). It suggests there may be a relationship between imagery ability and subjective experience of recollection. Here I predicted there would be a positive relationship between vividness of visual imagery measures and the vividness of each modality.

2.2. Method

2.2.1. Participants.

Data from 30 participants were originally collected. The final sample consisted of 27 undergraduate students from the UEA (7 male; *Mean* age = 20yrs, *SD* = 1.68). All participants were right-handed, had normal or corrected-to-normal vision and hearing, and reported no history of neurological disorder. Three participants of the original 30 were removed from data analysis, one due to too many trials being rejected from pre-processing (19.4%) and two due to a high proportion of noisy channels (24 channels in both cases).

2.2.2. Materials and apparatus.

For EEG acquisition, a 64-channel active electrode system (Brain Products GMbH) and amplifier (BrainAmp MR 64 PLUS) was used with a nylon cap (BrainCap-64 channels). Participants sat approximately 70cm from a 24" computer monitor (resolution 1920 x 1080 pixels) with speakers set up either side of the monitor. The task was presented using E-Prime 2.0 and a standard keyboard was used for responses with right hand rested on the numerical pad.

A total of 9 clips were used: three audio, three visual, and three multimodal (audio-visual) clips. The stimuli were the same as that used in the episodic memory task in Bonnici et al. (2016) where nine nouns were selected based on their association with either visual, audio, or both audio and visual features. Each word had a corresponding clip that represented the word in the Bonnici et al. (2006) and we obtained these same stimuli clips from the author. Audio clips were presented through speakers, visual clips silently on a computer screen, and multimodal clips that presented audio and visual simultaneously. For example, for the word 'cloud' a silent, time lapse video clip was used displaying a blue sky with white clouds moving across the screen.

Paper versions of the Vividness of Visual Imagery Questionnaire (VVIQ; Marks, 1973) and Bucknell Auditory Imagery Scale (BAIS; Halpern, 2015) were used to measure levels of individual visual and auditory imagery respectively. The VVIQ is a 16-item questionnaire which asks participants to picture a scene and rate how vividly they can mentally picture aspects within this scene on a scale of 'no image' to 'as vivid as if in real life'. The BAIS is similarly a self-report measure that asks participants to rate vividness and control for sounds described in a series of statements (e.g., think of a beach, and consider the sound of the waves crashing against rocks). There are a total of 28 questions in the BAIS: 14 regarding vividness (BAIS-V) and 14 regarding control (BAIS-C). See Appendix B and Appendix C respectively.

2.2.3. Procedure.

In a study phase before EEG acquisition, participants learnt to mentally replay each of the 9 clips. These clips were learnt in three blocks of modality: audio clips played through speakers, visual clips displayed on a computer monitor, and audio-visual clips with both audio and visual aspects presented simultaneously. The presentation of each learning blocks was counterbalanced across participants. The clips were a representation of the word shown and participants were shown the word followed by the six second clip and asked to recall the clip as vividly and consistently as possible. They were first shown the clip and instructed to mental replay the clip with their eyes close in their own time. They were then trained to recall the clip within a six second recall window so that the memory would be a consistent length to that of the clip and unfold as such. Participants were asked to replay the clip as vividly as possible and to try to be consistent with their replay as possible. This procedure allowed each clip to be thoroughly learnt and recalled in the same temporal manner.

Between the study phase and the retrieval phase participants were given a short comfort break and the EEG system was set up. The time period between finishing the study phase and beginning the retrieval phase was typically around 40 minutes.

In the retrieval phase, participants were presented with a word and instructed to vividly replay the associated clip they had learnt earlier (see *Figure 2.1*). After the 6 second recall window, a beep sounded to indicate participants should open their eyes. They were then asked to rate how vivid their replay was on a scale of 1 to 4, with one being low vividness and four being extremely vivid. Following this, they were asked to rate how consistent they felt the replay was to the original clip, with one not very consistent and four being very consistent. Lastly in each trial participants were also asked to indicate the modality of their replay (1 for audio, 2 for visual, or 3 for audiovisual). Participants completed a total of 144 trials displayed over 8 blocks and were given short breaks in between each recording block. This minimised participant movement during recording and ensure concentration during the task. At the end of the retrieval phase, participants were given a full debrief.

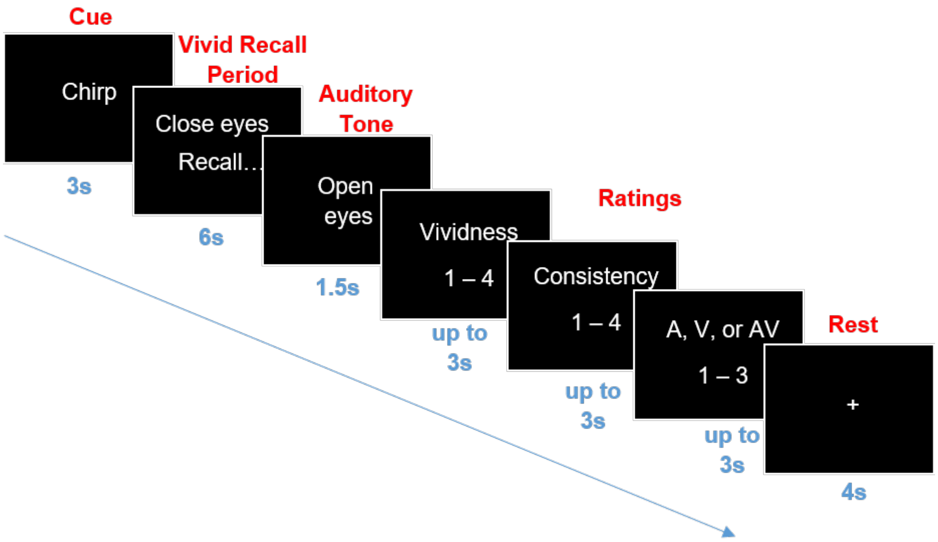

Figure 2.1. Timeline of a single trial in the retrieval phase. This trial has the cue word for an audio clip.

2.2.4. EEG data acquisition.

2.2.4.1. EEG recording.

Continuous EEG was recorded from a 63-channel active electrode system (Brain Products GMbH). Electrode placement was according to the extended international 10/10 system. Eye movements were recorded from an electrode placed below the left eye using an electrode taken from electrode site Oz. Sampling rate was 500 Hz and electrode site FCz was used as a reference.

2.2.4.2. EEG preprocessing.

Offline EEG data was preprocessed using the EEGLAB toolbox (eeglab14_1_2b) on Matlab 2017b. Linear tread was removed with a high pass filter of 0.1 Hz. A notch filter at 50 Hz and 100 Hz was applied to reduce line noise and a low pass filter of 130 Hz was run. In order to clean noisy segments, ASR was run on the continuous data. ASR is a technique that establishes a portion of data with minimal noise and then applies a sliding window to classify the data as either within normal variance or as high variance by comparison (see Mullen et al., 2015 for a more detailed overview of steps). Bad channels were identified using the ASR technique and interpolated via the triangulation method of nearest neighbour. Three participants were removed at this stage due to either too many channels interpolated, or a large portion of data determined as too noisy. Of the remaining 27 participants, approximately 4 channels were interpolated per person (Mean = 4.22, SD = 3.87). The ASR was run again following the interpolation to determine any remaining bad segments of data. Next, the data was visually inspected and trials that still contained artefacts were manually rejected. Average re-referencing was applied before finally epoching from the appearance of instructions to close eyes to 6000ms after.

2.2.5. Analysis.

2.2.5.1. Time-frequency decomposition.

The STUDY function in EEGLAB was used to examine event-related power changes at the channel level using event-related spectral perturbation (ERSP; see Delorme & Makeig, 2004). The ERSP method divides the epoch into short overlapping windows and calculates a moving average of the power spectra which is then normalised; this procedure is averaged across trials to produce the average ERSP (Makeig, 1993). Here, a Fast Fourier Transform (FFT) was computed with a 6 cycle wavelet in 500ms Hanning-tapered window across the window of replay (0ms to 6000ms). Power was calculated for 65 log spaced frequencies between 3 and 68 Hz. A total of 300 time points spaced approximately in steps of 12 seconds were extracted. Baseline normalisation was conducted by subtracting the average of the whole epoch replay window. This was due to the presence of a cue before replay and an auditory tone following replay. Frequencies of interest were as follows: Theta (4 – 8 Hz), Alpha (9 – 12 Hz), Beta (15 – 30 Hz), Gamma (32 – 68 Hz). The average power for each frequency band was divided into 14 time bins of 250 milliseconds from 1250ms to 4750ms using a custom script. The mean spectral power for conditions is represented in decibels (dB).

2.2.5.2. Significant testing.

To assess significance of comparison, non-parametric permutation tests were performed using the Matlab function 'statcond'. Briefly, this method of analysis shuffles the data from two conditions and then carries out paired samples t-tests at each point to (e.g., mean power for multimodal and visual conditions across participants). This creates the sampling distribution under the null hypothesis that there is no difference, and the process is repeated 2000 times. Following the permutation testing, correction for multiple comparisons was conducted by the False Discovery Rate (FDR) method using the 'fdr' function to determine significant electrode sites in each time bin. FDR is an acceptable method of correcting the probability when conducting multiple tests (e.g. Nobel, 2009).

2.3. Results

2.3.1. Behavioural results

2.3.1.1. Vividness.

We examined differences in average vividness ratings across modalities (see *Table 2.1.*). A one-way repeated measures ANOVA showed there was a significant difference in vividness ratings across the 3 modes of recall ($F(2,52) = 10.528$, $p < .001$, $\eta_p^2 = .288$). 95% confidence intervals are reported in square brackets. Paired sample t-tests showed a significant difference between audio and multimodal vividness ratings ($t(26) = -3.731$, $p = .001$ [-.589, -.170]), and audio and visual vividness ratings ($t(26) = -3.502$, $p = .002$ [-.551, -.143]). Vividness ratings for audio clip recall was significantly lower compared to both visual and multimodal recall. There was no significant difference between visual and multimodal vividness ratings ($t(26) = .449$, $p = .657$ [-.114, .178]).

To see if there was a relationship between the vividness ratings for modality in our participants, we ran correlations between all conditions (see *Table 2.2*). There was a strong positive relationship between vividness rating for multimodal and visual conditions ($p < .001$). There was a moderate positive relationship between vividness ratings for audio and multimodal ($p < .001$), and for audio and visual ($p < .001$) conditions. See *Figure 2.2*.

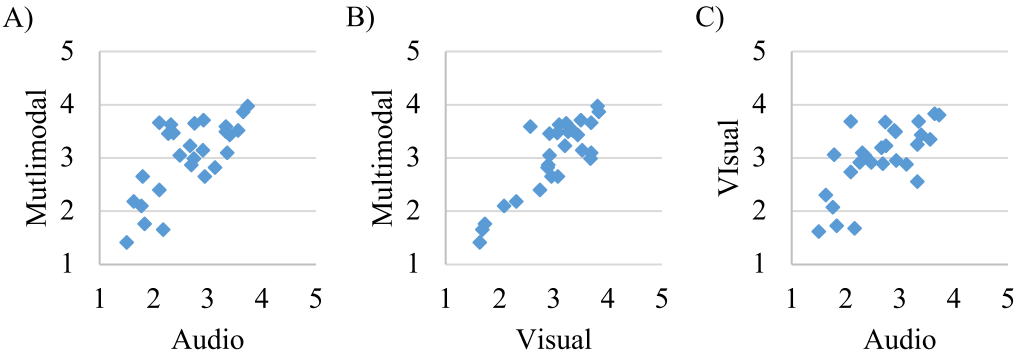

Figure 2.2. Average vividness ratings for each modality and their relationship to each other ($p < .001$ in all cases). A) shows the relationship between multimodal and audio vividness ratings. B) shows the relationship between multimodal and visual ratings. C) shows the relationship between visual and audio rating.

2.3.1.2. Consistency.

A one-way repeated measures ANOVA was run to compare average consistency across modalities (see *Table 2.1.*). There was a significant difference across mode for consistency ratings ($F(2,52) = 17.286$, $p < .001$, $\eta_p^2 = .399$). Follow-up paired sample t-tests showed a significant difference between audio and multimodal consistency ratings ($t(26) = -5.271$, $p < .001$ [-.65, -.285]), and audio and visual consistency ratings ($t(26) = -4.187$, $p < .001$ [-.597, -.204]). The consistency ratings for audio clip recall was lower significantly lower compared to both visual and multimodal recall. There was no significant difference between visual and multimodal consistency ratings ($t(26) = .939$, $p = .357$ [-.08, .215]).

We also examined the relationship between the average consistency ratings for each mode (see *Table 2.2.*). There were strong positive correlations between audio and multimodal ($p < .001$), and visual and multimodal ($p < .001$) consistency ratings. There was a moderate positive correlation between consistency ratings for audio and visual conditions ($p < .001$). See *Figure 2.3*.

Table 2.1. Means and standard deviations (SD) of vividness and consistency ratings for each modality.

	Vividness Mean (SD)	**Consistency** Mean (SD)
Audio	2.64 (0.66)	2.42 (0.60)
Visual	2.99 (0.64)	2.76 (0.67)
Multimodal	3.02 (0.71)	2.88 (0.67)

Table 2.2. Pearson's Correlation values for average vividness and consistency ratings by each modality.

Vividness			
	Audio	**Visual**	**Multimodal**
Audio	-	.684	.702
Visual	-	-	.855
Multimodal	-	-	-
Consistency			
	Audio	**Visual**	**Multimodal**
Audio	-	.699	.741
Visual	-	-	.845
Multimodal	-	-	-

NB: $p < .001$ in all cases.

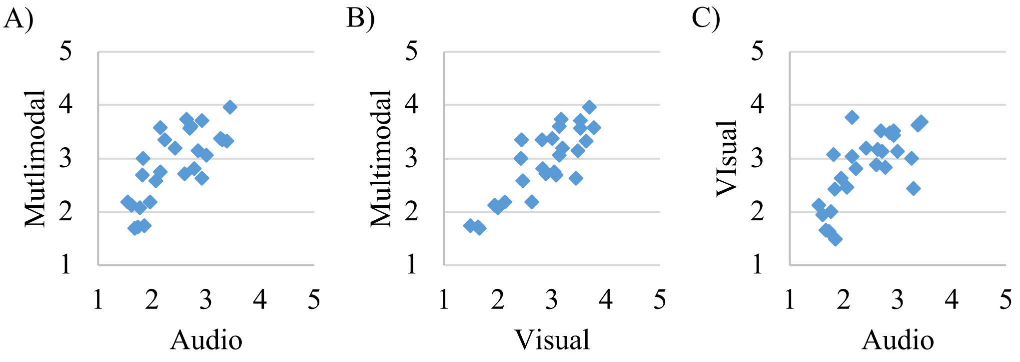

Figure 2.3. Average consistency ratings for each modality and their relationship to each other ($p < .001$ in all cases). A) shows the relationship between multimodal and audio consistency ratings. B) shows the relationship between multimodal and visual consistency ratings. C) shows the relationship between visual and audio consistency ratings.

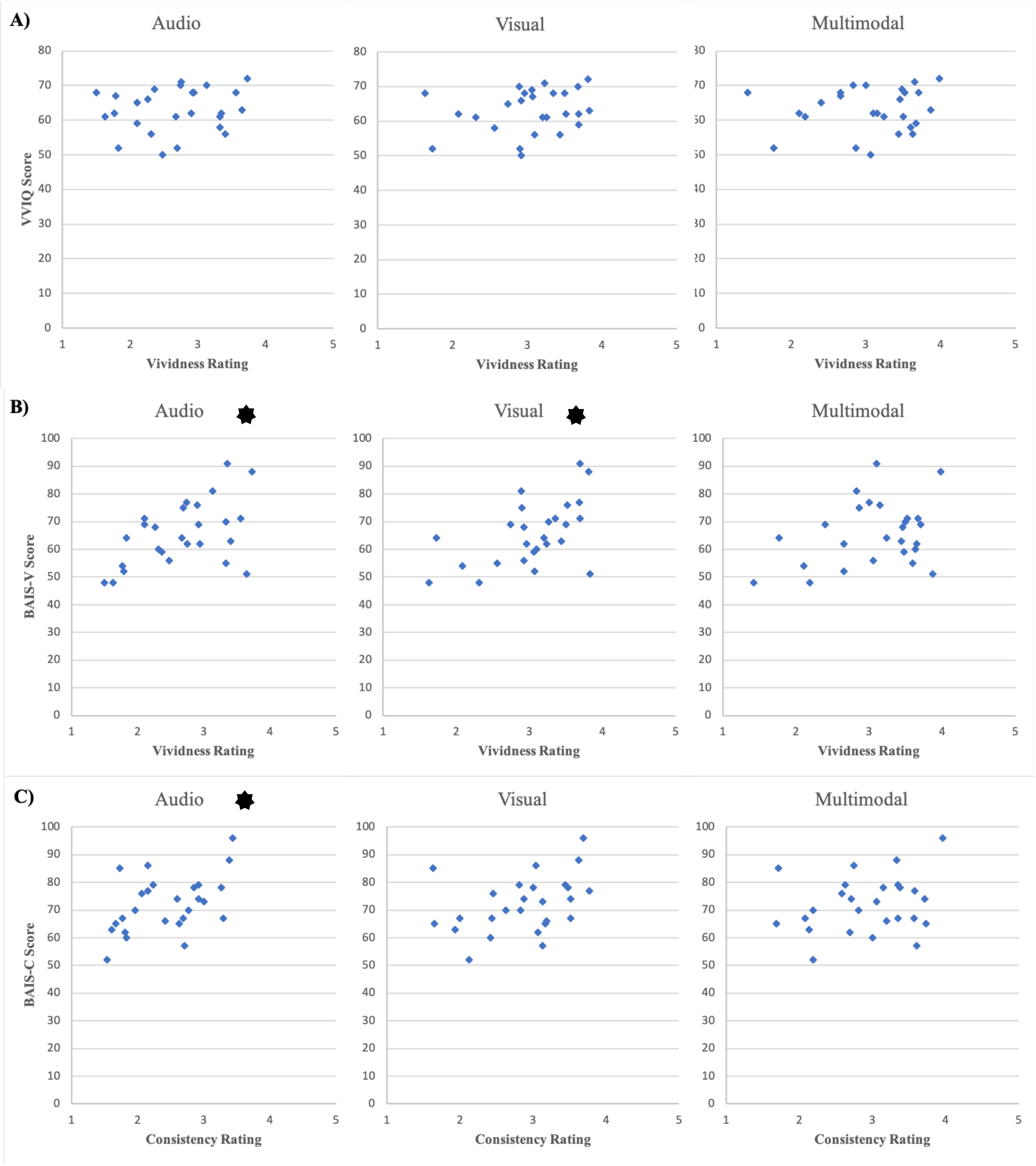

Figure 2.4. Scatterplots of scores on each imagery measures the relationship to average vividness and average consistency ratings for each modality. Significant

relationships ($p < .05$) are marked with a star. A) Scatterplots for the VVIQ scores and average vividness ratings for audio, visual, and multimodal conditions. B) Scatterplots for the BAIS-V and average vividness ratings for audio, visual, and multimodal conditions. C) Scatterplots for the BAIS-C and average consistency ratings for audio, visual, and multimodal conditions.

2.3.1.3. Imagery measures.

The self-reported scores of vividness of visual imagery were compared to the overall vividness ratings across modalities. VVIQ scores did not correlate with overall vividness for audio, multimodal, or visual replay (all $p > .05$). We examined the relationship between individuals' scores on the BAIS-V scale and the mean scores of vividness of each modality. There was a significant correlation with scores on the BAIS-V scale and overall auditory vividness ($r(24) = .517$, $p = .007$). Similarly, there was a significant correlation between BAIS-V and overall visual vividness ($r(24) = .539$, $p = .005$). There was no association between BAIS-V and mean multimodal vividness ($r(24) = .328$, $p = .539$). Imagery control scores from the BAIS were looked at with the consistency of each modality. The BAIS-C scores and auditory consistency were significantly correlated ($r(24) = .469$, $p= .016$). There was not relationship between BAIS-C and average multimodal or visual consistency (both $p > .05$). See *Figure 2.4.* for scatterplots).

2.3.2. EEG results

Time-frequency analysis was restricted to trials where the indicated mode of replay matched that of original modality for the clip. The segment of interest was limited to the 6 seconds of replay that followed the presentation of the cue and started from the point of instruction to close eyes and recall.

2.3.2.1. Theta.

A comparison of mean power in the theta band (4 – 8 Hz) across all electrodes and all time windows was conducted. To determine if theta power differences were present depending on modality, I compared multimodal replay against audio replay. This contrast did not reveal any significant difference at any electrode site in any of the 250ms time windows (all $t < 4.8$, $p > .05$). A comparison of theta power between multimodal replay and visual replay also did not reveal any significant difference (all $t < 4.32$, $p > .05$). The unimodal conditions were also compared; this contrast did not find any significant difference between visual and audio replay conditions (all $t < 3.63$, $p > .05$).

2.3.2.2. Alpha.

To determine if there were power decreases in the alpha band (9 – 12 Hz), mean power was compared across conditions. No significant differences were found when contrasting multimodal replay to audio replay (all $t < 4.85$, $p > .05$), or to visual replay (all $t < 3.16$, $p > .05$). A comparison of audio to visual replay similarly found no significant differences (all $t < 3.46$, $p > .05$).

2.3.2.3. Beta.

The mean power in the beta band (15 – 30 Hz) was compared across modalities. Multimodal replay was compared to audio, showing no significant differences (all $t < 4.85$, $p > .05$). Similarly, a comparison of multimodal to visual replay showed no significant differences (all $t < 3.16$, $p > .05$). Comparison of beta power for the unimodal conditions also found no significant difference in power between visual and audio replay (all $t < 3.46$, $p > .05$).

2.3.2.4. Gamma.

To determine if there were modality differences in the gamma band (32 – 68 Hz), multimodal replay was compared to audio and visual. Both contrasts revealed no significant differences in gamma power at any electrode site for any time window (multimodal – audio: all $t < 3.43$, $p > .05$; multimodal – visual: all $t < 3.12$, $p > .05$). A comparison of the unimodal conditions also found no significant difference (audio – visual: all $t < 3.08$, $p > .05$).

2.4. Discussion

The primary aim of this study was to compare power differences in memory replay for multimodal and unimodal clips. I focused on frequency bands theta (4–8 Hz), alpha (9–12 Hz), beta (15–30 Hz), and gamma (32–68 Hz). I looked at 64 electrode sites across 250ms time windows to determine if any power differences occurred and where they may be localised in topography and timing. We expected to find increases of power in both theta and gamma bands, and decreased of power in alpha and beta power when comparing multimodal memory replay to unimodal conditions of auditory and visual. However, this was not the case and in the present study, we found no significant differences after correcting for multiple comparisons.

2.4.1. Behavioural findings.

Although the EEG results did not reveal what was expected, the behavioural data did demonstrate some interesting results that were not anticipated. Both average vividness and consistency ratings were lower for audio replay when compared to visual and multimodal replay. It suggests that the memory replay for auditory memory is less vivid and not as stable as the encoded event. This is in contrast to the findings of Bonnici et al. (2016) who did not find a significant difference in vividness ratings between modalities. This study used the same method of training to learn the clips, as well as the same episodic memory stimuli, as reported in Bonnici et al. (2016), it is therefore surprising we did find a difference in vividness ratings.

One possibility for our finding of lower vividness and consistency for audio replay compared to multimodal and visual could be due to the strength of memory performance not being wholly equivalent across all modalities. Memory for visual items has high recognition accuracy even at short presentation periods (Standing, 1973; Brady, Konkle, Alvarez & Oliva, 2008). In contrast, performance in auditory memory tasks seems to be poorer than that of visual memory (Bigelow & Poremba, 2014; Cohen, Horowitz & Wolfe, 2009; Cohen, Russ & Gifford, 2005; Jensen, 1971). Only when visual stimuli are severally degraded does memory performance of visual and audio material equate (Cohen, Horowitz & Wolfe, 2009; Visscher et al., 2007). In this study we used realistic clips to simulate auditory and visual information that could be encountered in everyday life. While degrading that stimuli may have produced more equality between the auditory and visual conditions, it would not be representative of a realistic situation of which participants then access and replay in episodic memory. It thereby stands that in everyday memory, auditory memory may not be as reliable and linked to a reliving experience when experienced it isolation.

A further consideration is that auditory memory performance is seemly worse at longer retention times (Bigelow & Poremba, 2014). In the present study the clips were learnt in three blocks, one for each modality, and the order of encoding was counterbalanced across participants. Because of this we cannot give a precise time of delay between encoding of each modality type and point of recall. Overall, the time period between learning all clips and beginning the recall tasks was approximately 40 minutes. It is possible that the retention of the audio clips as rich as they were at encoding were not retained as reliably as the multimodal and visual clips due to the retention time required.

This study did find a relationship between the ratings for the modalities. There were significant positive correlations between audio and multimodal, visual and multimodal, and audio and visual for both vividness and consistency. Taken together, it suggests that averaged higher ratings in one modality would mean averaged higher ratings in both others. It is interesting that we still find this relationship even though audio clips were less vivid and consistent. It suggests that participants treat the modalities equally but that scores for the auditory modality are generally lower in comparison to the other two conditions. It is possible that auditory memory alone is just not equivalent to visual or multimodal memory replay.

The relationship between the vividness and consistency ratings with the individuals' imagery measures we collected provide some interesting outcomes. We did not find any association between the score on VVIQ with any modality. It suggests that the self-report imagery scores of vividness ability may not have any association with how vividly someone is likely to experience each modality. On the other hand, we did find that the BAIS-V, a measure of auditory imagery vividness, was associated with higher scores on auditory as well as visual vividness ratings. Even though this measure focuses on auditory imagery, it suggests that there is close relationship between audio and visual imagery that may be hard to untangle. However, this does not explain the lack of association to multimodal vividness. This creates an interesting paradox as the multimodal stimuli requires a combination of audio and visual components. If the vividness ability is related to the vividness of visual and auditory elements as individual component it is at odds with the absence of a relationship between vividness ability and multiple replay vividness. It may be that this particular vividness measure may not be valid for modalities beyond the auditory domain. However an alternative explanation may be that individual imagery ability impacts differently for single modalities compared to integration of multiple modalities.

2.4.2. Theta.

I predicted that theta power would be greater for the multimodal replay of episodic memory as compared to audio and visual replay. Theta power has been associated with context judgements around parietal cortices (e.g., Guderian & Duzel, 2005; Strunk et al., 2017) and information maintenance around frontal cortices (Klimesch, Freunberg, Sauseng & Gruber, 2008). Therefore, I expected power differences in theta to be maximal around fronto-parietal electrode sites as context was reinstated and maintained. I predicted this would be greater for multimodal replay due to the greater requirement of integration between sensory information. The present work did not find any significant difference in theta band power when comparing any of the modalities. This was the case for all time windows across all electrode sites. The absence of a significant difference between sensory modalities suggests that theta power may not be sensitive to the modality of information within an episodic event. This is line with suggests theta power reflects domain general memory processes (Hanslmayr, Staudigl, Aslan & Baunl, 2010; Staudigl, Hanslmayr & Bauml, 2010). The present work expands this supposition to sensory modality in episodic memory replay.

Previous studies have found that theta may not be sensitive to material type but is to memory load (Khader & Rosler, 2011). This presents an interesting paradox in the context of the present study. Within multimodal episodic replay it is a reasonable idea to expect there is a greater memory load due to the requirement of processing two sensory modalities. Thus, you would expect greater widespread theta power for multimodal compared to unimodal conditions. On the other hand, if theta is not sensitive to material then there would be no difference in theta power between the multimodal and separate audio and visual conditions. It is possible that for memory replay, the role of theta is that of a general control process and power increases linked to memory load is specific when the load is within one sensory modality, explaining why we found no theta differences present in this work.

There is the possibility that participants may have unintentionally associated a visual image along with the audio content. The ratings of vividness and consistency for the audio condition were lower than that of multimodal and visual conditions, suggesting that replay of auditory content alone is challenging. If the audio and multimodal conditions both held audio and visual components to process it could explain why there were no difference in power. Although this would not explain the lack of any difference between the visual and multimodal conditions, unless this happened too for the visual memory. This seems less likely as memory for visual stimuli alone is generally very good.

Another possibility that could account for the absence of any significant difference may be due to the time window of interest in this work. Strunk et al. (2017) found theta power increases at 400 to 600ms for young adults and 400 – 800ms for older adults. Yet following this, there was a decrease in theta power around 1000 – 2000ms in both age groups and was greatest around posterior electrodes. It suggests that an early theta synchronisation effect (approximately 400 – 800ms after cue onset) is relevant for successful recollection, but this increase demonstrated in theta power is not sustained. However, this investigation was not assessing dynamic stimuli that required memory replay as was the case in the present study. The drop in power after the immediate cue may signify an end to control related processes as participants have successfully made a response decision. Khader and Rosler (2011) found theta power differences related to memory load, with power increases linked to greater load. Taken together, it would suggest that the dip in later theta power they demonstrate at a later time window may not be relevant to memory replay but rather a reflection of reduction in cognitive load in this study design as the memory context has already been successfully established.

Overall, we suggest that the absence of a theta power difference between unimodal and multimodal sensory modalities provides support that the role of theta in episodic memory is domain general control processes that are not sensitive to variations or increases in the number of sensory modalities.

2.4.3. Gamma.

I hypothesised that there would be greater gamma power, particularly around parietal regions, for multimodal recollection than both unimodal conditions. In this study, we did not find a significant difference in gamma band power when comparing any of the modalities. This was the case for all time windows across all electrode sites. One possible reason for the absence of any significant differences could be due to the gamma frequency window we defined. The parameter of gamma in this study was defined as 32 to 68 Hz taken from Cohen (2014). However, boundaries can vary between studies. There is evidence to suggest that the frequency range within gamma can vary depending on task and cortical areas linked to the task (Morgan et al., 2011). For example, high-frequency (>70 Hz) gamma activity has been linked to visual grouping (Vidal et al., 2006) and feature binding (Morgan et al., 2011). The band used here was arguably low-frequency (<70 Hz) gamma and therefore why no difference was found between the multimodal and unimodal conditions as expected for gamma.

Due to the design of the study, I cannot rule out the hypothesis that gamma oscillations do play a role in feature binding (Damasio, 1989; Morgan et al., 2011; Varela, 1995). A plausible explanation would be that binding of components is required to successfully replay the event regardless of modality, suggesting that gamma is not sensitive to the sensory modality of auditory or visual replay. Previous work has found greater gamma activity when manipulating visual-spatial features compared to manipulating a single feature in static stimuli (Morgan et al., 2011). It is possible that because the episodic event investigated in this study was a dynamic stimulus for all conditions, temporal binding had to occur; that is, the feature within the unimodal conditions had to be bound together to form a continuous representation. For example, one stimulus in the visual condition was that of clouds moving across the screen. Dynamic replay could require a series of feature manipulation to occur such as the shape and location of moving cloud.

Additionally, gamma power has been connected with a rich memory state of recollecting rather than familiarity (Burgess & Ali, 2002). Our hypothesis was generated on the assumption that episodic memory is a rich and multimodal experience. We therefore predicted greater gamma power for the replay of multimodal compared to unimodal, anticipating that the multimodal condition would be an example of a rich multimodal event and result in a great reliving experience. The lack of difference between multimodal replay and both audio and visual replay suggest that this is not the case; the modality of recollection does not have a relationship to gamma power.

2.4.4. Alpha and Beta.

Due to the evidence suggesting low frequency decreases in power are related to inhibitory control process in memory and material specific reactivation, I predicted a decrease in power for the multimodal replay compared to visual and auditory replay of episodic memory clips. However, no significant differences were found across modalities within alpha (9 – 12 Hz) or beta (15 – 30 Hz) frequencies, at any time window or electrode site. This result is surprising as if a decrease in power is linked to the representation of stored information, we would expect a focus of desynchronisation in the modalities examined here for the corresponding sensory location. Based on the theory that left parietal sites are involved in integration (see Bonnici et al., 2016; Seghier, 2013; Yazar et al., 2017 etc.), one would expect a maximal decrease at parietal sites for the multimodal condition where integration of representations is proposed to occur. The absence of a significant difference in the present study suggests that replay across sensory modalities may not be reflected in alpha and beta desynchronisation.

2.4.5. Limitations and future directions.

While the present work focused on the experience of reliving episodic memory through mental replay, there is one particular limitation with the present method that should be addressed. The design relies greatly on participants being honest in their mental replay of each clip following the cue word. Because we did not have an objective measure, there is no impartial way to confirm that the clip was truly replayed and reconstructed as reliving an event as we hoped was achieved. To account for this, participants were debriefed at the end of the task and asked to indicate how they found the task. We also removed trials whereby mode of replay was incorrect, interpreting it as an indication of failure to replay in the manner learnt at encoding. All participants indicated they completed the task and felt they had learnt the clips sufficiently during the debrief. While these steps mitigate some possibility that participants may not have actually completed the memory task, without an objective measure it cannot be a certainty. For example, there is the possibility of demand characteristics whereby a participant indicated they did recall a clip in the associated modality when in fact they did not but recognised it as supposed to be in the modality learnt at encoding.

An additional comment made by many participants during the debrief was the difficulty of the audio clips compared to the multimodal and visual clips. This observation is reflected in the behavioural data with lower ratings of vividness and consistency for the audio condition compared to visual and multimodal. It further highlights the unequal nature of auditory stimuli compared to the visual domain. However, in the study by Bonnici et al. (2016) using the same method of learning and retrieval as well as the same clips produced no difference in vividness ratings. It is possible that in this study the participants did not engage in the same manner with the learning task, accounting for the difference between the samples.

One consideration to note regarding the findings of this experiment and the conclusions that can be drawn is that the programme of analysis was performed at a whole-brain level. Additional analyses focusing on targeted regions may have indeed revealed different results. For example, focusing on the temporo-parietal junction region containing the angular gyrus that is implicated in audiovisual integration would be an interesting region to examine. While EEG methodology does not have asgreater precision as that of other neuroimaging methods such as fMRI, advanced analysis techniques could define regions on an activity based level to define a more targeted region of interest.

A further consideration regarding the design is the limits bounded by the time-frequency analysis. We did not look at the pre-replay due to any contamination caused by activity elicited from the cue word. Similarly, the end of the replay epoch was signally by an auditory tone. Therefore, these segments could not be used as a baseline in analysis. Instead, baseline correction was done by averaging the activity of all trials to create a baseline and subtracting that from each modality. A more elegant way to determine what oscillations were present for each modality would be to compare to a baseline recording. In order to avoid data mining in the present investigation we did not do this comparison as well as the comparison between modalities. This may provide an interesting insight into modalities replay alone before comparisons across the sensory modalities.

As with many oscillation studies, the conclusions that can be drawn are correlational rather than causational. That is to say that although we examine the stimulus induced oscillations, we cannot be certain our results are due to the oscillations ‘causing’ the memory replay rather than a result of the memory itself. Further research is needed to pursue more causational directionality. Techniques such as transcranial magnetic stimulation (TMS) are one way to explore this. TMS can disrupt the regular neuronal firing of a cortical location and the behavioural consequences can be examined to determine the role a region may have in a function. With careful design and lab set up it is also possible to conduct TMS and EEG simultaneously, an interesting direction for future exploration when assessing multimodal memory in future.

2.4.6. Conclusion.

To conclude, the present study explored the neural correlates of dynamic mental replay of both unimodal and multimodal conditions. The aim was to investigate differences in spectral power across frequency bands (theta, alpha, beta, and gamma) comparing multimodal, auditory, and visual modalities. This was to establish if oscillatory dynamics reflected a difference based on sensory modality in episodic memory. Although we predicted increased power for theta/gamma, and decreased alpha/beta for multimodal over unimodal conditions, our results did not find this to be the case. I conclude that the absence of modality related power differences in theta support the hypothesis that the role of theta is domain general for memory and not sensitive to modality. The results for an absence of alpha/beta desynchronisation are harder to explain. It is likely that the design of the study may have inhibited determining fine-tuned material representation therefore further work is needed to more precisely unpick how oscillations support both the dynamic replay of memory across modalities. Future work could focus on regional based analysis to determine if nuances exist in specific cortical regions.

Chapter 3

-

A TMS investigation into the role of the angular gyrus in multimodal feature integration.

3.1. Introduction

Episodic memory is defined by a rich reliving experience, usually accompanied by multiple modalities and a sense of reliving. In the previous chapter we examined the neural patterns underlying episodic memory replay for audio, visual, and multimodal event memory. The next area to be considered is the behavioural consequences of disrupting brain regions that contribute to the episodic recollection of items with both unimodal and multimodal features. Emerging research suggests that the left angular gyrus (AnG) has an important role in episodic memory, including that of a site that binds together sensory information into a unified representation which then enables a vivid sense of subjective reliving (e.g., Moscovitch et al., 2016; Simons et al., 2010; Yazar et al., 2017). Imaging studies show activation in the AnG for items with multimodal feature but not for unimodal features alone (Bonnici et al., 2016). This would suggest that multimodal features of an item are enough to require AnG activation for integration and in turn subjective recollection, but this remains to be tested.

The research question I address in this experimental chapter is whether the qualitative experience of recollection, as measured by a reflective confidence ratings of source memory, are reduced for items that have high multimodal features when stimulation is applied to the angular gyrus. Using transcranial magnetic stimulation (TMS), we create a virtual lesion over the angular gyrus and compare responses to a recognition and source memory task to stimulation of a control stimulation site. I begin this chapter by highlighting differences in measures of components within episodic memory, with a focus on a distinction between objective and subjective aspects of memory recollection. I go on to discuss accounts of the functional importance of the parietal cortex in episodic memory and what the role of the angular gyrus in particular may be; I also evaluate what we can determine from both patient and TMS studies in regard to the causal role of angular gyrus in episodic memory. Then, I provide a summary of key parameters that need consideration for a TMS investigation into episodic memory and summarise the present investigation.

3.1.1. Object and subjective episodic memory.

Episodic memory is far more complex than simply whether an episode is recollected correctly. In order to know if we have successfully remembered an event or piece of information, we can also reflect on the memory retrieval itself. Accuracy is important as an objective measure of whether successful retrieval occurred. Equally valuable is the subjective experience or phenomenology of the retrieval. For example, take Mandler's (1980) butcher on the bus scenario: you recognise a face as being familiar but are unsure why, therefore you search further memories for context about how you know that person and who they are. Whilst objectively you may be correct that you have met this person before, the experience of remembering this information involves trying to find the source of knowing this person and thereby establishing they are your butcher.

Recognition memory, as the name would suggest, is the ability to judge if an item has previously been encountered. In a study phase items are learnt, followed by a test phase where participants are asked if an item has been shown before. Recognition memory paradigms are a useful method for examining objective and subjective aspects of memory. Dual process theories of recognition memory (e.g., Wixted & Mickes, 2010; Yonelinas, 2001) propose two distinct memory process signals: recollection and familiarity. Recollection is described as retrieval of the studied item with additional qualitative information about the context in which it was learnt. Familiarity is defined as a sense of past occurrence but does not have any contextual information associated with it. Both recollection and familiarity can support a recognition judgement of whether an item is recognised as 'old' or 'new'. However, source memory judgements about recognised items require retrieval of information about the contextual features at learning and therefore is thought to depend on recollection rather than familiarity. In theory, the source memory judgement can provide an objective measure of the participant's memory experience. The exact details behind the dual process is somewhat debated. Particularly as to whether the signals are based on a threshold or continuous process (Norman, 2010; Wixted & Mickes, 2010). Despite this, the main concept holds that recognition memory can occur with or without retrieval of contextual information, and that a memory can be experienced in different manners.

A dual process approach often utilises a remember/know paradigm (Tulving, 1985) requiring participants to indicate whether they believe the item presented is either recollected (remember the episode) or is familiar (recognise the item, but do not recall the episode). One possible draw back using this paradigm is the timing of responses. Familiarity is generally a fast response, whereas recollection is a slower and evolving experience as more contextually relevant memories are accessed. It is possible that participants may give answered based on initial familiarity signals but still have recollection processes on going. Additionally, the binary response does not distinguish between different levels of a possible ‘remember’ judgement.

Another way to examine the retrieval experience is through confidence judgements. This approach suggests that confidence covaries with the quality of the source information being retrieval (see Rugg & King, 2018). Confidence of source judgement is strongly associated with source judgement accuracy (Mickes, Wais & Wixted, 2009). In this manner, confidence acts as a substitute for the amount of ‘recollected’ information about an episode and thereby assesses the quality of the qualitative information available at retrieval. However, it is worth noting that remember/know judgements and confidence ratings are not strictly equivalent (see Martin et al., 2011).

I argue that investigating both the objective and subjective aspects of an episode is important for understanding the mechanisms that support episodic memory. Retrieval-related activity in the left parietal cortex appears to be indicative of qualitative information about a prior experience rather than the accuracy of recognition judgments (Rugg & King, 2018; see also Chapter 1.4.3.). Understanding the impact of disruption on the qualitative experience of memory is necessary for determining its significance in episodic memory and for developing possible interventions in both healthy ageing and memory disorders. In the next section we review the role of the parietal cortex and its relation to subjective and objective aspects of episodic memory.

3.1.2. The functional role of parietal cortex in retrieval.

The role of the parietal cortex in episodic memory has garnered increasing interest in the past three decades. Previously the contribution of the parietal cortex in memory had been overlooked, largely due to parietal lesions resulting in less apparent memory deficits compared to other brain areas such as the medial temporal lobe. However, growing evidence particularly from neuroimaging studies has demonstrated that parietal activity regularly occurs in successful retrieval of episodic memory (Wagner et al., 2005; for reviews see Rugg & King, 2018; Sestieri, Shulman & Corbetta, 2017). The presence of parietal activation in neuroimaging studies suggests a role in memory function, yet patient studies show accurate episodic memory performance despite parietal lesions (Simons et al., 2008). This contradiction presents an interesting enigma in the precise role of the parietal cortex is in episodic memory.

Several theoretical accounts discuss the role of lateral parietal cortex, including the angular gyrus, in memory. For example, that of an episodic “buffer” (Vilberg & Rugg, 2008), a component of the working memory model that stores multimodal information (Baddeley, 2000); or as accumulator area for mnemonic decisions (Wagner et al., 2005). In contrast, the subjective experience account posits the role of the parietal cortex is to enable a subjective experience of rich reliving (Moscovitch et al., 2016; Simons et al., 2010). The angular gyrus has also been proposed to act as a convergence zone where integration of multimodal information from other sensory cortices occurs (Damasio, 1989; Shimamura, 2011) and it is this mechanic of integration into a coherent representation that supports a vivid subjective re-experience (Moscovitch et al., 2016; Simons et al., 2010). These accounts hold the assumption that the angular gyrus represents retrieved information in some capacity. Alternatively, an attentional account posits that the role of the angular gyrus is to direct attention and that activation represents this attentional mechanism rather than memories being represented (Cabeza et al., 2008).

Neuroimaging studies that examine patterns of voxels have indicated a representational account is a possibility. For example, Bonnici et al. (2016) used multivoxel pattern analysis and could distinguish mental replay of individual multimodal clips within the angular gyrus, but notably not the unimodal ones (audio and visual independently). It supports a representational account that mnemonic information is represented in the angular gyrus. An attentional account would suggest the same attentional mechanism would be used for each clip and therefore cannot explain the differentiation between each individual multimodal memory item.

It also demonstrates the area’s sensitivity to multimodal episodic memory, but not single sense episodic memory, which is in line with other evidence that greater posterior parietal cortex activity is observed for contextual rich recollection (Bonnici et al., 2016; Shimamura, 2011).

Patient studies add further insight into the subtle yet important role of the parietal cortex in episodic memory. The advantage of patient studies over imaging studies being that direct inferences regarding the role of the parietal cortex can be assessed, albeit with some caution. For example, in patients with bilateral parietal lobe damage, free recall of autobiographical memory recollection is impaired but cued recall appears intact (Berryhill et al., 2007). Additionally, recognition memory also appears to be preserved despite parietal damage (Ciaramelli et al., 2010; Haramati et al., 2008; Simons et al., 2010). A commonality across these patient studies is the presence of reduced subjective confidence whilst objective recollection of contextual details is still intact (Davidson et al., 2008; Hower et al., 2014). It demonstrates access to episodic memory but with a failure to appreciate the qualitative features (Ciaramelli et al., 2017).

Results from patient studies support a causal role of the parietal cortex in memory related to the subjective experience. Across three experiments comparing bilateral parietal lesion patients and healthy controls, Simons and colleagues (2010) found no differences in accuracy of source memory judgements. This was the case for both encoded auditory information (experiments 1 and 2: speaker gender of spoken sentences) and the visual information (experiment 3: coloured pictures of everyday objects). Further, the difference between experiments 1 and 2 was that in the second experiment attention was not directed towards encoding the gender and thereby reducing the relevance of it at encoding for the subsequent source retrieval judgement, suggesting it is not a deficit of bottom-up attentional capturing. Critically, across the experiments there was a reduction in confidence for source memory judgements for the patients compared to controls.

A key feature of recollection is the retrieval of multiple features of an episode (Tulving, 1985). Therefore, Ciaramelli and colleagues (2017) investigated the parietal role in integrating perceptual and spatial features in episodic memory. They examined the accuracy and subjective experience of patients with posterior parietal cortex damage and age-matched controls in a recognition and source memory task.

Words were presented in two possible colours and at different locations on a screen. Overall, they found a main effect of response, with higher confidence ratings associated with ‘remember’ rather the ‘know’ response. Patients and controls gave similar numbers of ‘remember’ responses, but patients were less likely to be highly confident about their response. The amount of remember responses given to correct multiple-feature recollection was lower for patients than controls, despite source memory performance for both colour and location being similar. It highlights an evaluative response difference between patients with parietal lesions and controls.

Overall, patient studies provide support for the view that the lateral parietal cortex has a causal role in recollection, focused on its qualitative aspects. However, several notes of caution are worth mentioning briefly. Firstly, the nature of lesions mean that the precise boundary of damage is not controlled and therefore the exact centre of damage responsible for the observed deficit is hard to determine. Parietal lesions in particular are generally large and cover several regions. Secondly, functional reorganisation could have occurred in the cortex of these patients. Thirdly, it cannot be ruled out that there is a role of damaged area in encoding so any recollection deficit of post-lesion learnt material could be a result of failed encoding rather than retrieval. Transcranial magnetic stimulation (TMS) is a neuroscientific technique that can overcome some of these challenges. TMS also allows causal inferences to be made about a brain region by creating temporary disruption of a controlled area of the cortex. It removes some ambiguity over cortical regions involved as the target area can be chosen. Further, it can allow to investigate the role of the parietal cortex in retrieval specifically, as stimulation can be conducted after encoding has taken place.

A limited number of studies have utilised this technique for examining the role of the parietal cortex in episodic memory and more specifically the left angular gyrus. For example, Sestieri et al. (2013) compared performance for source memory when rTMS stimulation was applied to either the IPS, posterior angular gyrus, or vertex in an online paradigm (see section below for more detail about the different types of TMS). At encoding, participants were shown pictures and asked either if they were man-made or natural (animacy) or how much they liked the picture (pleasantness). They used signal detection theory to analyse their findings which examines sensitivity (ease of detecting signal against ‘noise’) and bias (likelihood of one response over another) of decision making. They found a small reduction in recognition sensitivity following angular gyrus stimulation compared to the superior parietal lobule (SPL) condition. Also following angular gyrus stimulation, whilst confidence remained the same, there was a bias for responding with ‘pleasantness’ as the source condition rather than ‘animacy’ following angular gyrus stimulation compared to SPL and sham conditions. In an alternative rTMS offline paradigm where cortical disruption occurs for an extend time rather than time-locked to stimulus presentation, Yazar et al. (2014) found a reduction in source judgement confidence following angular gyrus stimulation compared to vertex. Both studies suggest a causal role of angular gyrus in subjective confidence about source judgements.

The left angular gyrus has been proposed to have a role in binding together multimodal information into a coherent representation, a process that in turn allows a vivd subjective sense of reliving (Moscovitch et al., 2016; Simons et al., 2010). A study by Yazar, Bergström and Simons (2017), examined the role of the angular gyrus in multimodal retrieval. Participants encoded a natural scene with an embedded object (e.g., a ball in a park), while hearing the object word (e.g., “ball”) spoken concurrently, and made a pleasantness judgement. Following either angular gyrus or vertex stimulation, participants were shown the word previously spoken at encoding and asked to make a recognition judgement followed by a source judgement if relevant. The possible source conditions were single source (such as just speaker gender), within-modality (such as speaker accent and gender), or across-modality (such as object position and speaker gender). The main finding was a small reduction in source accuracy when retrieval required both auditory and visual information to be combined. There was no difference in performance when combination of information concerned one modality. This is in line with a proposal that the angular gyrus integrates modality information into a coherent whole for vivid reliving. Although it is somewhat at odds with Ciaramelli ’s patient study discussed earlier, where the integration of two visual features was enough to find a change in the subjective experiencing. One possible explanation for this difference is the methodology in subjective assessment. Source accuracy judgements assume that recollection is occurring and by extension integration too. Remember/know responses on the other hand require participants to make a subjective judgement. It is possible that the source accuracy judgement alone is not enough to examine subtle information about the qualitative memory state.

Drawing together the converging evidence from various cognitive neuroscientific methods leads to the suggestion that the role of the parietal cortex in recollection is of subjective nature, rather than determining successful memory retrieval. More specifically, the angular gyrus is a likely candidate in supporting this subjective experience through its integration of multimodal sensory information. Further examination of the integration by the angular gyrus is needed to determine its precise role. Yazar et al. (2017) look at multimodal integration for scenes, with an object embedded within, and speaker auditory information. Yet it is unknown if a single item with multimodal features still relies on the angular gyrus to integrate and inform subjective experiencing when recollecting that item. Bonnici et al (2016) found greater activation for angular gyrus in their multimodal item replay which would suggest that an item with multimodal features is sufficient to engage the angular gyrus for this purpose. This is the premise for the current investigation, outlined further at the end of this section. Next I summarise key information about TMS and explain how the technique is used in studies of episodic memory to instruct how I will be using it in the current study.

3.1.3. Principle of TMS in episodic memory.

Transcranial magnetic stimulation (TMS) is a neurostimulation method based on the principles of electromagnetic induction whereby a changing magnetic field is used to induce an electrical field to a portion of the brain. TMS affects neuronal processing by inducing currents in neuronal networks: an alternating current in a coil is placed over the scalp which invokes brief magnetic field “pulses” which, in turn, invoke a current in axons beneath the coil. Whilst the concept of using magnetic fields to stimulate the human brain was present in the late 19th century, it was not until 1985 that Antony Barker and colleagues introduced TMS as it is known today (Barker, Jalinous & Freeston, 1985). Since this development TMS has been a widely used technique, both in clinical and research setting, due to its ability to cause temporary and reversable disruption. Its main advantage in research being as a way to establish a causal link between a region and task outcome; the hypothetical function of a region can be tested as the TMS produces disruption of typical neural activity. However, there is a large variety of parameters to consider when looking at how TMS be utilised in the study of episodic memory.

Generally, TMS protocols can be divided into two types: single or paired-pulse TMS, and repetitive TMS (rTMS). rTMS can be applied as a continuous single pulse train with regular intervals. Alternatively, it can be patterned whereby short bursts of pulses are interleaved with short pauses of no stimulation. Critically, rTMS has been used to both enhance and impair behaviour and cognition by modulating cortical excitability (Pascual-Leone et al., 1998). It is the interaction between parameters such as timing, frequency, and intensity that is essential in determining whether a protocol is inhibiting or exciting the typical activity in a region of interest. Understanding the consequences of manipulating parameters is necessary in the assessment of how neurocognitive processes support episodic memory (Yeh & Rose, 2019). Furthermore, it has consequences on the conclusions that can be drawn about the outcomes. For example, knowing that a combination of parameters creates inhibitory neural firing and observing reduced performance in a task compared to a control site, you can support a hypothesis that the target site plays a role in supporting that behavioural outcome. This has reaching implications for inventions for healthy ageing and clinical disorders related to memory. When we further understand how the parameters of TMS can be used in research, we can then consider how they can be utilised in interventions.

The main parameters which we consider in the following review include timing, intensity, and frequency of pulses. The technical parameters of timing, frequency, and intensity have to be carefully considered both for the affect they cause and to ensure a safe protocol for participants. Guidelines, set out by Wassermann (1998) and more recently updated and reviewed by Rossi and a consensus of TMS experts (2009), outline safe parameters for the application of TMS. These guidelines framework the appropriate combinations of intensity, frequency and inter pulse train interval that can be used for a safe protocol. We briefly summarise the parameters and their relationship to the study of episodic memory and relate to our present investigation (for a recent review and meta-analysis see Yeh & Rose, 2019; for earlier reviews see Grafman & Wassermann, 1998; Manenti et al., 2012).

The timing of TMS stimulation needs careful consideration and can be dependent on the research question being addressed. Stimulation can be delivered ‘online’, where stimulation occurs during the completion of a task. Alternatively, it can be ‘offline’, where it is used to induce a change in activity for a duration past the stimulation period and participants experience a brief sustained period of stimulation before then completing a behavioural task. Online stimulation immediately effects brain activity whereas offline stimulation can have after-effects of up to an hour (Bergmann et al., 2016).

Selection of frequency can be based upon previous protocols suggested to either enhance or inhibit cortical excitability. High frequency or intermittent theta burst (iTBS) protocols are believed to enhance, whereas low frequency or continuous theta burst (cTBS) protocols to suppress cortical excitability (Huang et al., 2005; Hallett, 2007). An alternate way to use stimulation frequency to modulate cortical activity that is worth noting is via oscillations, although this is not the approach taken in the present investigation. For example, Luber and Lisanby (2014) suggest that through alternating neural oscillations and driving neural entrainment it can influence any communication between brain regions and cognitive outcomes.

Intensity of stimulation is measured as a percentage of the maximum stimulator output (MSO). Typically for rTMS protocols, first the intensity needed to produce a consistent visual motor response in the hand from stimulation to the motor cortex is determined. This seeks to find the lowest threshold required to reliably produce the response. The intensity for the rTMS stimulation is then calculated as a percentage of the MSO needed for the motor threshold. Although it is worthwhile to note here that this method of defining intensity assumes the intensity needed to produce a motor response via stimulation of the motor cortex would also be sufficient to produce similar disruption in another cortical region.

TMS is an effective non-invasive brain stimulation technique with clear advantages over patient studies such as the reversible lesions in a localised region. However, there are some limitations in regard to its spatial resolution and depth. The nature of the technique means that it cannot be used to stimulate medial or subcortical structures as the depth of the field reaches approximately 2.5cm. Some questions also remain as to the exact field of neurons that are affected by TMS stimulation. Recently, Romero, Davare, Armendariz and Janssen (2019) examine the spatial extent of TMS in rhesus monkeys. They applied online single pulse TMS to parietal regions and found spiking activity in single neurons less than 2cm in diameter. It suggests that the spatial region the stimulation impacts is generally focal and unlikely to be impacting neighbouring cortical regions beyond the targeted location.

Above we have briefly summarised the key principles of TMS that should be considered. TMS is an incredibly useful technique for the purposes of memory research. As long as safe parameters are followed and the area of interest is on the surface level of the brain, TMS is a powerful tool to test the hypothesised role of a region in memory recollection. The present investigation uses a commonly used form of patterned offline rTMS known as continuous theta burst stimulation (cTBS) that was original outlined by Huang et al. (2005) and hypothesised to inhibit cortical excitability. This cTBS protocol delivers bursts of 3 pulses at 50Hz with an inter-pulse interval of 200 milliseconds (within the theta range of 5Hz, hence the name) for a continuous train of 40 seconds. Huang and colleagues originally used this protocol for stimulation of the motor cortex, however it has also been used in other regions including the angular gyrus (e.g. Bonnici et al., 2018; Yazar et al., 2014; 2017) which is the target of our present investigation. We also follow the same stimulation intensity thresholding as these studies at 70% of the motor threshold. By utilising similar parameters to previous research on the angular gyrus and episodic memory of modalities we can directly compare our findings and conclusions.

3.1.4. The present study.

Our key area of interest in the present investigation was whether the integration of multimodal features by the angular gyrus applies to a single item which is considered to have both audio and visual features and thereby impacts subjective experiencing. Work by Bonnici and colleagues (2016) would suggest that the multimodal nature of an item alone is enough to engage the angular gyrus in an episodic memory task. Previous work has focused on the integration of features within an event such as object position and speaker accent, whereas we focus on single items with multiple features (for example a waterfall). Additionally, we look at confidence ratings as our index of subjective experience.

In line with the prediction that the angular gyrus is involved in the retrieval of qualitative information related to the context of encoding, but not related to successful recognition, we expected no difference in recognition accuracy between angular gyrus and vertex stimulation. Similarly, we did not expect a difference in confidence responses for the recognition judgements for audio, visual, or multimodal conditions as this recognition judgement does not require contextual information to be retrieved. In contrast, if the role of the angular gyrus is to integrate sensory features for successful reliving, we would expect a difference in source accuracy judgements between angular gyrus and vertex stimulation for the multimodal condition, but not for the unimodal conditions. If this binding is the mechanism that enables subjective experience of recollection, then this should be reflected in reduced confidence in source judgements due to being unable to bind the audio and visual features of an item at recollection. Hence, we predicted that there would be a reduction in confidence for source recollection following AnG stimulation compared to vertex for the multimodal condition. This reduction in confidence should be present for the multimodal condition but the not the unimodal conditions as no integration of features would be required.

3.2. Method

3.2.1. Participants.

Twenty-five participants took part in the study (12 female; M = 21.96 years; SD = 2.24; age range = 18 - 28). A total of 26 participants were recruited via an online paid participant panel advert, but one participant failed to return for the second testing session therefore their partial data was removed from further analysis.

Each participant had normal or corrected-to-normal vision, normal hearing, and were right-handed. At recruitment stage, all participants were screened by means of a TMS safety screening questionnaire to determine the possibility of an adverse reaction to TMS. This safety screening questionnaire is based on considerations of safe parameters outlined by a consensus of TMS experts (Rossi et al., 2009). Participants were excluded if they had a history of seizures or epilepsy (including family history), had a history of brain related injury or illness, suffered from frequent and severe headaches, had a history of fainting or syncope, were taking psychiatric or neuroactive medication (e.g. antidepressants, antihistamines), had metal in their body or implanted devices (e.g. surgical clips, pacemaker), were pregnant, or held a heavy goods driving licence.

Participants visited the lab twice, each visit lasting approximately an hour. The first visit was slightly longer to allow time for participants to familiarise themselves with TMS and ask any questions. The safety screening questionnaire was administered at the start of each session. This was to ensure no changes had occurred to the original screening and to determine that there was no alcohol consumption, participation in another TMS study, or sleep disruption 24 hours prior to the session. We also asked participants to refrain from consuming caffeine for the 1 hour preceding the session.

Ethical approval for the project was given by the School of Psychology Ethics Board at the University of East Anglia and participants gave informed consent before each testing session. Participants were reimbursed for their time in accordance with established rates set by the department.

3.2.2. Materials.

A word list of 240 nouns that were associated highly with auditory, visual or audio-visual features were assembled from previous research (see Bonnici et al., 2016) and our own short pilot data which rated the words on auditory and visual features (see Appendix D). Auditory dominant words were considered as having significantly more auditory than visual features, and visual dominant words had more visual features than auditory. Whereas audio-visual words had equal visual and auditory features. Words were displayed in black Courier New font size 18. The word list was then halved, half was used for the encoding task and the other half for the recognition task, with an equal number of words for each modality.

For the audio trials, there was a total of 40 sound clips sourced from an online sound bank (freesound) and edited in Audacity software to be 2 seconds in length. Similarly, for the visual trials 40 pictures were located from creative commons sources and edited in photo editing software to have a white background

(400 by 400 pixels). Multimodal trials were a combination of 40 sound clips and 40 pictures (sourced and edited as above) played and displayed simultaneously. See *Figure 3.1.* for examples of stimuli.

Figure 3.1. The top row of images are examples of the visual stimuli presented alone for visual trials (Frame; Crown; Button; Balloon). The bottom row of images are examples of the visual stimuli presented in multimodal trials (Train; Owl; Harp; Hammer). These 4 visual stimuli were accompanied by an auditory clip that semantically matches. For example, the hammer accompanied by the sound of a hammer striking a nail.

3.2.3. Procedure.

Participants were tested on two separate occasions, one week apart. One session was the experimental condition where stimulation was to the left angular gyrus and the other session was the control condition where stimulation was to the vertex. The session order was counterbalanced across participants. The same task procedure of a study and test phase was conducted at both sessions, with half the stimuli for each session, presented on a laptop using E-Prime (2.0). These too were counterbalanced resulting in four possible combinations of stimulation and stimuli list. In each session, participants first went through the safety forms and gave informed consent. They then completed the study phase, followed by stimulation before a final test phase for items. The whole session lasted no more than an hour in total.

3.2.3.1. Task procedure.

In the study phase, participants were shown a word followed by an item, either a sound, a picture, or both, that represented the word. For example, if participants saw the word ‘alarm’ it would be followed by an audio clip of an alarm, whereas for the word ‘fountain’ following it would be a picture of a fountain accompanied by the audio of running water in a fountain. Participants were asked to rate whether they found the item (second stimulus) pleasant or unpleasant using left and right arrow keys.

In the test phase, participants completed an old/new recognition paradigm. Participants were shown a word and instructed to think whether they experienced an item with the word. If they had experienced an item with the word, then it was an “old” word and if they had not, then they should indicate it was a “new” word. Specific emphasis was put on recall of the item experienced with the word during the study phase. This was in order to ensure recollection of the whole event (word cue plus item) rather than simply familiarity of the word cue. Additionally, if a word was indicated as being ‘old’ participants were also asked what the presentation mode of the clip was: ‘audio’, ‘visual’, or ‘both’ using the left, up, and right arrow keys respectively. After each question they were also asked how confident they were with their answer on a scale of one to five (with one being not confident at all and five being very confident). Participants were encouraged to utilise the full range of the confidence scale and to answer all questions as accurately and as quickly as possible. See *Figure 3.2*.

Both the study and test phase had a short practice section of four trials prior to commencing the task to ensure that participants understood the instructions and were happy with the layout of a trial and response requirements. This occurred for both sessions. A full debrief was provided at the end of the second session.

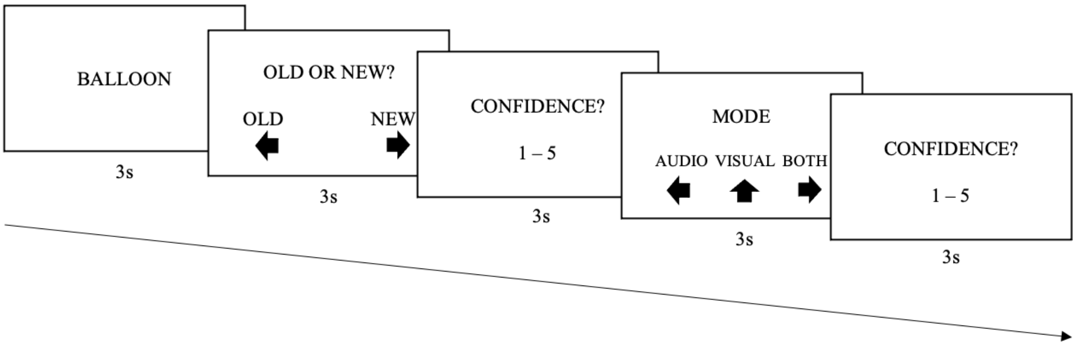

Figure 3.2. Example timeline of a trial in the test phase. In this example, an 'old' response would have been given in order for the mode question to also appear.

3.2.3.2. cTBS procedure.

An offline standard conditioning protocol of cTBS was used as per previous studies (e.g. Bonnici et al., 2018; Huang et al., 2005; Yazar et al., 2014, 2017). Stimulation was delivered using a Magstim Rapid (Whitland, UK) with a standard 70mm diameter figure-of-eight coil. Three pulses at 50 Hz repeated at 200ms intervals for 40s resulting in a total of 600 pulses, were delivered at one of the target stimulation sites for each session at 70% of resting motor threshold. The frequency, intensity, and duration of the protocol was all within outlined safe limits (Rossi et al., 2009). The stimulation sites were angular gyrus (MNI co-ordinates -43, -66, 38) and vertex (MNI co-ordinates 0, -15, 74). These co-ordinates were picked based on previous research using the same locations in investigations of angular gyrus function (Bonnici, Cheke, Green, FitzGerald & Simons, 2018; Yazar, Bergstrom & Simons, 2014; Yazar, Bergstrom & Simons, 2017). Vertex stimulation was selected rather than a sham stimulation condition in order to produce the same sound and sensation as at the target region and has been demonstrated as a suitable control condition (Jung et al., 2016).

At the start of the first session, the resting motor threshold for each participant was assessed using the right first dorsal interosseous hand muscle. Location of the left hand motor region was estimated as 5-6cm laterally and 1-2cm anterior from the vertex based on previous research (see Buccino, Sato, Cattaneo, Rodà & Riggio, 2009), with the coil first placed here and adjusted until the best site was determined. Motor threshold was calculated using adaptive parameter estimation by sequential testing (adaptive PEST) whereby a simple non-parametric algorithm is used to estimate the TMS motor threshold (Borckhardt et al., 2006; free software available at http://www.clinical researcher.org). An initial starting point was set to 50% with increments of 7% on each participant and adjusted until the minimum limit to consistently see muscle movement was reached. Once the resting motor threshold was determined, 70% of this figure was computed to be used as the intensity for the cTBS procedure for both sessions.

Using the neuro-navigation system software Brainsight (Rogue Research, Canada), the participant's head was co-registered to the MNI 152 average brain. This method uses infrared sensors to co-register the participants head with a 3D head model. Landmarks of the naison, LPA, and RPA were used as well as determining the frontmost, backmost, leftmost, and rightmost positions on the participant's head. Validation check of landmark points (i.e. naison, LPA, RPA) were aimed to be within 6mm to ensure good co-registration. To apply TMS, the researcher held the coil tangential to the scalp surface with the centre of the coil (i.e. the stimulation point) monitored via the neuro-navigation system to ensure it remained over the target site for the duration of the stimulation.

Participants were given a short rest period after stimulation and before starting the test phase to ensure the virtual lesion was created via the cTBS protocol. The length of any effect from a cTBS protocol is still debatable and often vary highly between individuals (see Huang et al., 2005). In a review, Wischnewski and Schutter (2015) establish that the effects of 600 pulse over 40s last up to 60 minutes after stimulation. Therefore, we ensured our test phase task would take a maximum of 30 minutes to ensure the virtual lesion created by the protocol was in effect.

3.3. Results

Planned comparisons tested for the presence of cTBS-induced performance impairments following angular gyrus stimulation compared to vertex stimulation. One-tailed alpha was set at 0.05. The use of one-tailed tests was considered suitable as we are testing for the presence of impaired performance and reduced confidence following stimulation to the AnG. Effect sizes were calculated using Cohen's *d*.

Mean reaction times were calculated for each participant; trials where reaction times were less than 250ms (3.37%) or a timeout occurred (0.67%) before the old/new response were discarded from further analysis. Reaction times falling 3 standard deviations above or below each participant mean for the old/new response were also discarded as outliers (1.63%).

Old/new recognition performance was calculated based on the proportion of correctly identified 'old' items. Similarly, source recollection performance was computed with the proportion of trials with correct identification of modality. Only trials following a correct recognition response were considered for the subsequent source recollection performance. Confidence was calculated as the proportion of trials with high confidence responses (button presses of 4 and 5) based on correct performance of the previous question. See Table 3.1., Figure 3.3. and Figure 3.4.

Table 3.1. Participants' accuracy on the old/new recognition and source recollection task.

	AnG	**Vertex**
	M(SD)	**M(SD)**
Old/New Recognition		
Audio	.86(.13)	.86(.13)
Visual	.93(.07)	.94(.07)
Multimodal	.93(.11)	.93(.10)
Old/New Recognition Confidence		
Audio	.90(.11)	.89(.11)
Visual	.97(.06)	.97(.05)
Multimodal	.96(.05)	.96(.05)
Source Recollection		
Audio	.80(.21)	.81(.14)
Visual	.96(.06)	.97(.05)
Multimodal	.84(.20)	.84(.14)
Source Recollection Confidence		
Audio	.74(.22)	.79(.20)
Visual	.94(.07)	.96(.05)
Multimodal	.92(.11)	.95(.07)

Note: AnG = angular gyrus, M = mean, SD = standard deviation. Calculated to 2 decimal places. Accuracy indicated as a proportion correct. Source recollection conditional to correct recognition and reflects the proportion of correct trials receiving a highly confident response of 4 or 5.

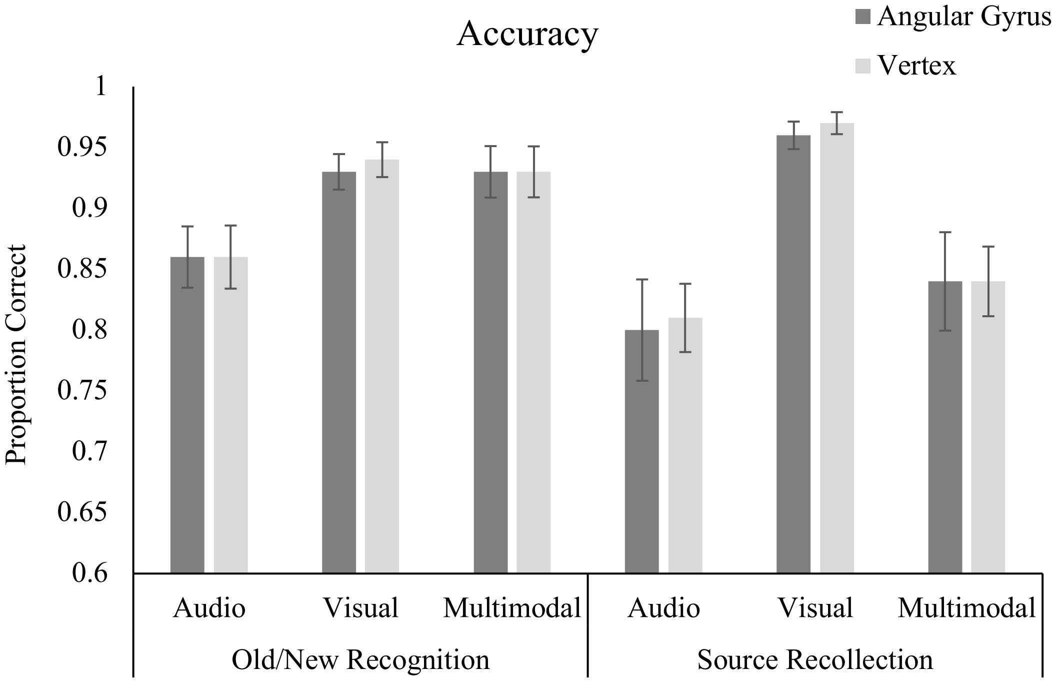

Figure 3.3. A graph of the proportion of correct judgments made for the old/new recognition and source recollection responses for each modality. Note that source recollection responses are conditional to correct responses at recognition. Error bars represent standard error.

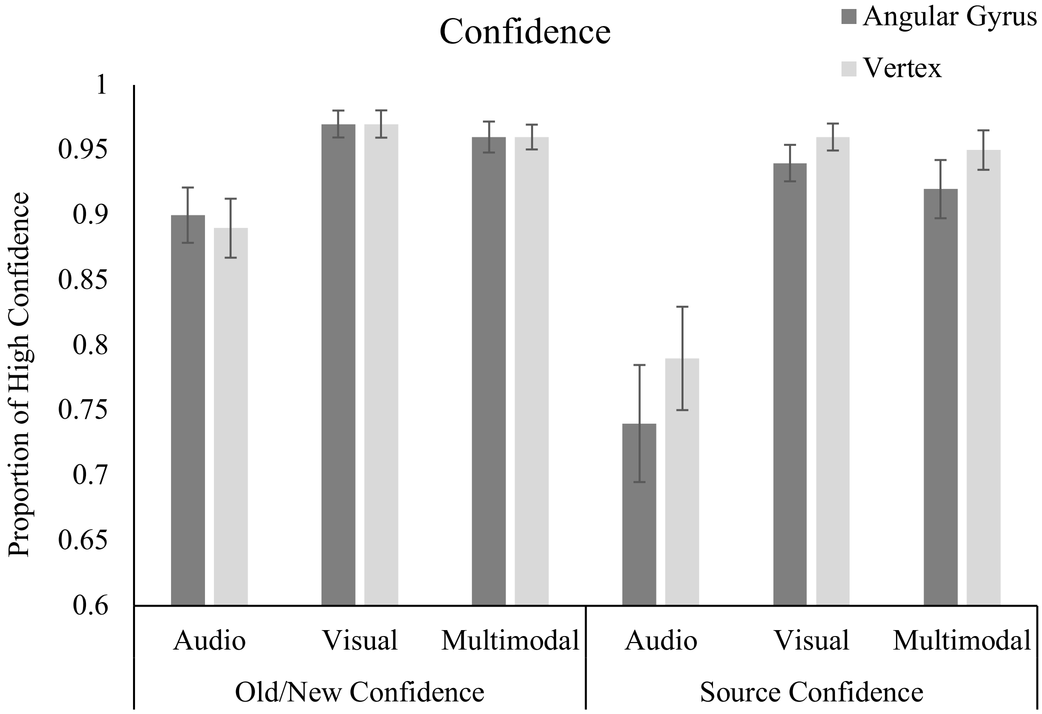

Figure 3.4. A graph of the proportion of high confidence judgments made for the old/new recognition and source recollection responses for each modality. Error bars represent standard error.

3.3.1. Old/New recognition.

Accuracy. For trials with only one modality, there was no change in performance accuracy when comparing AnG stimulation to vertex stimulation for audio, $t(24) = -0.047$, $p = 0.482$, $d=0.009$, and visual trials, $t(24) = -0.696$, $p = 0.247$, $d = 0.139$. As expected, there was also no reduction in hits between AnG compared to vertex stimulation for multimodal trials, $t(24) = -0.068$, $p = 0.473$, $d = 0.015$.

Confidence. There was no significant reduction in high confidence ratings for the old/new recognition following AnG stimulation compared to vertex stimulation in audio, $t(24) = 0.265$, $p = 0.397$, $d = 0.009$, visual, $t(24) = -0.331$, $p = 0.372$, $d = 0.139$, or multimodal trials, $t(24) = 0.251$, $p = 0.402$, $d = 0.015$.

3.3.2. Source recollection.

Accuracy. Examining source recollection accuracy, a repeated measures ANOVA with factors of modality (audio, visual, multimodal) and stimulation site (AnG, vertex) showed no main effect of stimulation site ($F(1,24) = 0.211$, $p = 0.65$) nor an interaction effect ($F(1.423,34.159) = 0.474$, $p = 0.625$; Greenhouse-Geisser corrected). There was a main effect of modality on source recollection accuracy ($F(2,48) = 15.998$, $p < .001$).

Due the main effect of modality, we compared source recollection accuracy for the multimodal condition and the unimodal conditions within each stimulation site. There was no difference in source recollection accuracy for multimodal and audio trials in both AnG and vertex conditions ($p > .05$). Source recollection accuracy for audio trials was lower than the visual trials for both AnG $t(24) = -4.042$, $p < .001$, and vertex conditions, $t(24) = -5.594$, $p < .001$. Similarly, the source recollection accuracy of multimodal trials was also lower compared to visual trials for both AnG, $t(24) = -3.305$, $p = .003$, and vertex conditions, $t(24) = -4.720$, $p < .001$.

Planned comparisons revealed no difference in source recollection accuracy for both the audio trials, $t(24) = -0.687$, $p = 0.249$, $d = 0.137$, and visual trials, $t(24)$

= -0.736, *p* = 0.235, *d* = 0.146, following AnG stimulation compared to vertex stimulation. AnG stimulation in the multimodal condition did not significantly reduce source accuracy when compared to vertex stimulation, *t*(24) = 0.364, *p* = 0.360, *d* = 0.073.

Confidence. A repeated measures ANOVA with factors of modality (audio, visual, multimodal) and stimulation site (AnG, vertex) revealed no main effect of stimulation site (*F*(1,24) = 2.228, *p* < 0.149), nor an interaction effect (*F*(1.387,33.296) = 0.332, *p* = 0.719; Greenhouse-Geisser corrected) on source recollection confidence. There was a significant main effect of modality (*F*(1.385,33.231) = 28.510, *p* < 0.001; Greenhouse-Geisser corrected).

Due to the main effect of modality, post-hoc tests were run on the source recollection confidence scores between the multimodal condition and each unimodal condition (audio and visual). This was done separately for the two stimulation sites to determine if there were subjective confidence differences across modalities in both the disruption and control stimulation sessions. Audio confidence ratings were significantly lower than multimodal confidence scores in both AnG, *t*(24) = 4.308, *p* < .001, and vertex conditions, *t*(24) = 3.77, *p* =.001 (two tailed). There was no difference between visual and multimodal confidences scores in either stimulation condition.

Planned comparisons showed there was no difference in high confidence source recollection confidence between AnG stimulation and vertex stimulation for the audio trials, *t*(24) = -0.969, *p* = 0.171, *d* = 0.194, or for the visual trials, *t*(24) = -0.7, *p* = 0.246, *d* = 0.275. Contrary to what we predicted, for the multimodal trials there also was no significant difference between the stimulation sites, *t*(24) = -1.375, *p* = 0.091, *d* = 0.141, as this only approached our alpha threshold, even if the mean difference in confidence ratings was in the expected direction.

3.4. Discussion

This study investigated whether the multimodal integration of audio and visual features for one item would recruit the angular gyrus and underlie the subjective remembering of recollection. We predicted that disruption of the angular gyrus using cTBS would reduce performance on a source memory judgement and confidence ratings for multimodal items but not for items that only had a unimodal feature. There was no difference in source memory accuracy for multimodal items after the angular gyrus was compared to a control site. Contrary to what was expected, there was no statistically significant difference in the proportion of high confidence source judgements. However, we did observe a trend in the data with a reduction in high confidence source responses following angular gyrus stimulation for multimodal items compared to vertex stimulation. It is a possibility that with more participants this effect may have achieved significance.

The source memory accuracy and confidence findings are at odd with some previous research such as the findings by Yazar et al. (2017). A key difference between this investigation and the present one was that we examined integration for multimodal feature of a single item rather than a scene. It is possible that the the angular gyrus has primarily a role for integration of scene representation into a coherent whole, and not for integrating multimodal features for a single object such as a fountain. Yazar and colleagues (2017) looked at integration of speaker accent/gender, and object position and side. Similarly, Ciaramelli et al.'s (2017) feature integration was that of word colour and location. From Bonnici et al.'s (2016) study that found angular gyrus activation for multimodal but not unimodal items, we predicted that the multimodal features of a single item would be enough to engage the angular gyrus. However, a key factor in the Bonnici study was the use of dynamic stimuli: all the stimuli were 3 second video clips of the item, such as a book opening, or a train passing by. Therefore, the presentation in the current study of a static object with accompanying audio may not be sufficient to engage the angular gyrus.

Another explanation of the difference in findings is that upon reflection of the procedure, the source judgement task of identifying modality may have caused some unintentional confound on the validity of the results. The items were chosen for the features they represented for each modality. For example, all the auditory items were rated and classified for their representation of highly auditory features. We used the word cue presented before each item as the cue word in the test phrase. However, there was no way to control for participants guessing at the source memory judgement. Thereby the source accuracy scores may not be reflective of a retrieval process but more of semantic memory for an object and the feature they believe would have been presented with that object. One would hope that the confidence rating would be lower for ‘guesses’ but there is no way to confirm this. A lower confident rating would thereby also be less valid as it would then not represent less qualitative information about the encoding episode.

Previous studies have suggested that the angular gyrus contributes to the subjective judgements and confidence in memory. For example, Yu, Johnson and Rugg (2012) compared retrieval-related angular gyrus activity measuring both Remember/Know and a source memory judgement. When participants made a ‘remember’ response, there was a significant difference in angular gyrus activity for highly confidence and low confidence response. There was no activity difference for low confidence ‘remember’ responses and ‘know’ responses. Similarly, Ritcher, Cooper, Bays, and Simons (2016) found that activity in the angular gyrus was not sensitive to vividness but did covary with precision of source memory feature retrieval. To my knowledge, previous studies looking at memory performance following TMS disruption to the angular gyrus have not examined confidence judgements. The source memory confidence judgements were intended to be reflective of the belief in the source decision and subsequently reflect the quality of the retrieved information. Whilst there was a trend in the expected direction with a reduction in the number of highly confidence trials, from this study we cannot conclude that disrupting the integration of multimodal features resulted in reduce confidence in the memory judgement and experience.

Another important consideration regarding the results is a potential lack of power. The final sample size of 25, although in line with other TMS investigation, may not be sufficient in order to detect what is likely a relatively small effect. This may explain the trend in the data of a reduction in confidence for multimodal items following angular gyrus stimulation compared to vertex. It is likely that an increase in the number of participants would achieve a significant finding as we had initially predicted. Linked to the point regarding limited power, the choice of localisation method means that we may have needed a greater sample size compared to other methods, such as using an individual’s MRI scan, in order to detect a significant difference (see Sack et al., 2009). We used a method that utilised average MNI152 co-ordinates and morphed the brain scan to each head. There is a larger amount of inter-individual variability between boundaries of the areas within ventral lateral parietal cortex (Caspers et al., 2006). Because we did not use individualised structural MRI scans or, even more accurate, individualised functional scans it is somewhat possible that we may have been slightly off target in stimulating the angular gyrus. The co-ordinates chosen were based on other studies targeting the region therefore it may not be the co co-ordinates that are problematic but the morphology of different head shapes to the generalised scan.

One possible method to overcome some of the design issues mentioned but using the same stimuli in future would be to ask participants to recall the subjective category they allocated the item to in the encoding task. In the present study, participants had to indicate whether they found the item pleasant or unpleasant. Asking for the recall of this contextual judgement made at encoding would ensure true recollection, rather than familiarity. It would also overcome the issue of presenting the item word which was highly associated with features of a particular modality. Adjustment of the task at test phase would also help overcome an additional challenge that developed over the period of data collection. The study was piloted to test task difficulty and the first two participants results were scanned to checked to ensure no computer collection errors or extremely high or low accuracy scores. Despite this initial pilot, the final results suggest that the task may have been too easy, resulting in memory performance approaching ceiling. Although increasing the number of items within the task may have increased the task difficulty, we were limited by the number of items we could present in one session due to the temporal limits of TMS effects possibly wearing off. A future design could consider testing each modality separately and over a greater number of sessions to increase the number of each test item.

Consistent with previous studies (e.g. Ciarimelli et al., 2017; Yazar et al. 2014; 2017), there was no difference in accuracy for recognition judgements or number of high confidence recognition judgements in either multimodal or unimodal conditions when comparing performance following angular gyrus and control site stimulation. A successful recognition judgement does not necessarily require contextual information to be retrieved or evaluated. It supports the conclusion that the angular gyrus is not required for the performance of recognition memory decisions. One unexpected, but not entirely unlikely, outcome was the finding that confidence rating of audio items was significantly lower than both multimodal and visual items.

Previous research indicates that while visual memory has a high accuracy and capacity (Brady, Konkle, Alvarez & Oliva, 2008; Standing, 1973), the same is not necessarily true for auditory memory. Cohen, Horowitz and Wolfe (2009) investigated auditory memory performance and observed that even when sound clips were paired with a corresponding object (thereby creating multimodal encoding), this did not improve recognition performance of the sound clip at test. It suggests a difference between visual and auditory memory. Additionally, it shows that multimodal encoding does not necessarily invoke multimodal retrieval. This may also explain why we found a main effect of source recollection accuracy; the source condition of visual items were more accurately recalled than that of auditory and multimodal items. Although Cohen et al (2009) did not directly test multimodal source recollection performance, it does suggest that visual conditions may be superior to both audio and multimodal conditions at encoding.

In the present investigation a finding of particular note is in the source recollection accuracy. We found no difference in the accuracy between multimodal and audio conditions but both these conditions are significantly lower than the visual condition. This work assumed that all modalities are equal at encoding, however, there are several challenges present constructing a truly unimodal or multimodal condition. One must consider that the encoding of an event is often never without that of visual information. For example during the study phase, the audio trials were accompanied by a fixation cross to look at. In this manner one could argue that this is not a ‘pure’ unimodal audio trial as, while the fixation cross is not linked semantically the audio information, it still inherently contains information encompassed within the visual domain. Additionally, while we may have displayed a picture accompanied with semantically related sound for the multimodal condition, we cannot be certain that both domains of modality were truly attended to and that one modality was not more dominant than the another.

In summary, this investigation did not find that angular gyrus disruption caused a reduction in performance of source memory judgements in multimodal feature integration. It did not support the hypothesis that multimodal integration is a mechanism of underlying subjective assessment of retrieved memory. The trend in reduced confidence for multimodal source judgement is likely reflective of some effect, however, the parameters of the current design were not sufficient to determine this.

Chapter 4

-

The contribution of object and spatial mental imagery in episodic memory

4.1. Introduction

A defining feature of episodic memory can be the re-experiencing of a past event in vivid detail as a multisensory experience (Wheeler, Struss & Tulving, 1997). Mental imagery can be described as the cognitive process of re-experiencing in the absence of external stimuli (Kosslyn, Ganis & Thompson, 2001). It is therefore reasonable to consider a link between mental imagery and episodic memory; both definitions comprise of recollection experience based on stored knowledge and without the presence of the external sensory information. Previous research has demonstrated a link between visual imagery abilities and the experiences of episodic memory (e.g. Greenberg & Knowlton, 2014; Irish, Lawlor, O'Mara & Coen, 2011; Rubin, Schrauf & Greenberg, 2003). Individuals who do not report the use of mental imagery also report a reduced sense of reliving when reflecting on past events (Greenberg & Knowlton, 2014). Vividness of visual imagery has also been correlated with the strength of event recollection (Rubin 2005), visual details, and representation of spatial information (D'Argembeau & Van der Linden, 2006).

In the previous chapters I explored the experience of episodic memory when recollection was of a unimodal or multimodal nature, examining confidence and vividness. Yet an underlying assumption was that the experience of replaying an event (Chapter 2) and recognition and retrieval of source context (Chapter 3) for unimodal and multimodal events were similar across all individuals. Individual differences in the presence of imagery is not a new idea but has received renewed interest more recently (see Chapter 1 for an overview). Additionally, the individual imagery differences present in Chapter 2 suggest that imagery ability may link to different modal components in episodic memory. In the present chapter I take an individual differences approach and examine how differences in visual imagery can impact the way we experience memory. I examine the contribution of imagery as two separate constructs of spatial and object imagery on different memory processes. Autobiographical memories are episodic events that have had an opportunity to be rehearsed and integrated into a personal schema. Therefore, in Experiment 1, I examine the contribution of imagery on event details and phenomenological characteristics of both recent and remote autobiographical memories to examine if imagery contribution varies for the age of an event being remembered. In experiment 2, I look at imagery contributions during an episodic memory recognition and spatial manipulation task to determine what impact imagery may have on a lab based memory task.

4.1.1. Conceptualising mental imagery.

Mental imagery can be described as the representation and experience of sensory information, often recalled from memory, and without the external source of stimuli (Kosslyn, Ganis & Thompson, 2001; Pearson, Naselaris, Holmes & Kosslyn, 2015). This mental stimulation can involve multiple modalities and is often referred to as “seeing in the mind’s eye” or “hearing in the mind’s ear” when discussing visual and auditory imagery respectively (Kosslyn, Ganis & Thompson, 2001; Kosslyn, Thompson & Ganis, 2006; Holmes & Mathews, 2010). Often, the term mental imagery is thought of in regard to describing just visual mental imagery but it important to note that mental imagery can occur in relation to all sensory information in the absence of an external source. For purposes of the current work, I refer to visual mental imagery when using the term mental imagery unless otherwise stated.

Historically mental imagery had been ignored due to methodological and theoretical reasons (see Pearson, Naselaris, Holmes & Kosslyn, 2015). Due to its internal nature, firstly measuring mental imagery was problematic. Secondly, the behaviourism era dismissed the presence of internal representations due to their unobservable nature. Additionally, the discussion as to whether information was represented pictorially or whether it was propositional knowledge about the world also slowed some research on imagery as a worthwhile pursuit to further research. This debate has on the whole been resolved, with acceptance that pictorial representation is possible (see Pearson & Kosslyn, 2015; although also see Pylyshyn, 2003). Now mental imagery is gaining more momentum, offering some interesting research implications as well as possible clinical applications (see Pearson, Naselaris, Holmes & Kosslyn, 2015).

Behavioural and neuroimaging methods have allowed further understanding of mental imagery. The development of validated self-report measures, such as the Vividness of Visual Imagery Questionnaire (VVIQ; Marks, 1973), have allowed quantitative investigation of imagery as a construct. There also appears to be an overlap between mental imagery and perception (Farah, 1989; Kosslyn, Ganis & Thompson, 2001); the mental picture works as a weak form of perception. Neuroimaging work suggests that mental images and perceptual images are similar even in the primary visual cortex providing strong evidence for a pictorial account of internal representation (for a review see Pearson, Naselaris, Holmes & Kosslyn, 2015).

However, there is some debate as to the exact meaning of this early visual cortex activation. Patients studies show intact V1 regions but a deficit in visual mental imagery (Moro, Berlucchi, Lercg, Tomaiuolo & Aglioti, 2008), and the reverse with cortical blindness in V1 but intact visual mental imagery (Bridge, Harrold, Holmes, Stokes & Kennard, 2012). This suggests that early visual areas do not have a causal role in visual mental imagery (Bartolomeo, Hajhajate, Lui & Spagna, 2020). Overall, it indicates that mental imagery is likely a widespread network recruiting cortical areas depending on several factors including task demand. It demonstrates that there is still much to understand and define in imagery, with focus needed on what is actually being examined.

There are several ways imagery can be conceptualised (see Richardson, 1999). The earlier description of mental imagery as a re-experiencing of sensory information without an external source can explain imagery as an internal representation but also as a phenomenological experience. For example, how vivid the experiencing of the mental image created is to the individual. Another way imagery can be thought of is as mnemonic strategy often discussed as visualiser versus verbaliser; that is the preference to use imagery as a memory aid. It can also be considered as an attribute of a stimulus, for example how concrete or abstract a stimulus is when thought about.

Each of these ways to think about imagery do have some overlap. Under the earlier definitions, they still all require the assumption that there is a reconstruction of an image in the mind’s eye, without the presence of an external stimulus, based on stored knowledge. The phenomenological experience requires assessment of image generation, the mnemonic strategy approach is an individual style of memory aid, and stimulus attribute refers to how easy something is to create an internal image. However, despite all being based on the notion that an internal representation exists, caution should be taken to avoid generalising across approaches. For example, someone may be described as a ‘visualiser’ if they have a preference for using image generation memory strategies over verbal strategies, yet they may not experience these mental images as vividly as say a ‘verbaliser’ may do if they chose to generate a mental image.

Kosslyn (1981) presents a computational theory of mental imagery that a surface representation exists, generated from stored deeper knowledge. This surface representation can then be operated on to perform other cognitive tasks. The generated image can be inspected, scanning parts or the whole to extract information (Kosslyn, Thompson & Ganis, 2006). Image transformation can occur on content and characteristics of the generated image. This can manipulate what is being generated (e.g. based on goals), or how it is generated (e.g. perspective). While mental imagery is being generated, inspected, and transformed it must also be maintained by reactivating the representation.

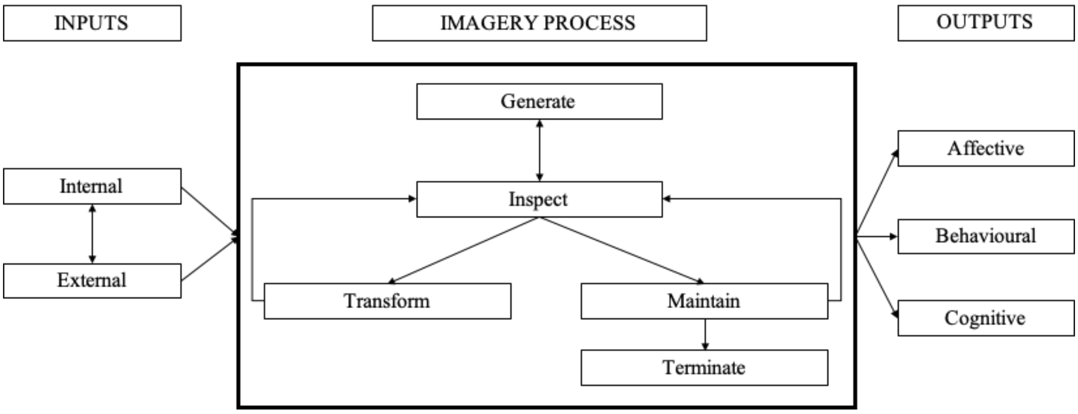

Figure 4.1. Interaction of imagery stages for imagery in sports performance (see Cummings & Eaves, 2018).

Although a model devised for imagery in sports performance, Cummings & Eaves (2018) outline the interplay between mental imagery processes clearly (see figure 4.1). This model exemplifies mental imagery as a complex construct and cognitive process comprised of several stages that evolve and develop an internal representation that can be assessed and impact outputs. To fully understand how mental imagery could interplay with episodic memory one must also have clarity on how mental imagery is being conceptualised in the context of a piece of research.

Additionally, the stage of the mental imagery process needs to be considered, such if an internal representation is being generated or maintained and reflected on.

A further consideration regarding mental imagery is whether mental imagery is a singular concept. Evidence points to mental imagery being more than just a unitary construct (Kosslyn et al., 2001; Thompson, Slotnik, Burrage & Kosslyn, 2009), suggesting it can be divided into object and spatial imagery as separate constructs (Blajenkova et al., 2006). Spatial imagery focuses on the imagined spatial relations between elements of a scene, whereas object imagery is in regard to the perceptual elements. For example, forming a mental representation of your kitchen would likely require spatial imagery to construct the layout of the sink relative to the cooker. Focusing on a specific feature within the kitchen such as the colour of the kettle would utilise object imagery to recreate perceptual features. This distinction appears to hold at a functional level (Farah, Hammond, Levine & Calvanio 1988; Logie, 2003), and at a neural level (Kosslyn, Ganis & Thompson, 2001; Mazard, Tzourio-Maxoyer, Crivello, Mazoyer & Mellet, 2004).

For clarity, in this work, I conceptualise imagery as the generation of an internal representation upon which a subjective phenomenological experience can occur. It is also worthwhile to note that mental imagery is not limited to accurate re-experiencing of memory. By definition it is the creation of a mental picture based on stored information which incorporates the creation of fictious imagined events too. For example, a stored representation of an elephant may be that it is grey, but mental imagery can pull stored information about the colour green to allow the generation of a mental image containing a green elephant. In this example, rather than an accurate representation of the semantic knowledge of what colour an elephant is.

4.1.2. Mental imagery and episodic memory.

Growing evidence suggests a link between visual mental imagery and memory. Visual imagery has been linked with a sense of reliving (Greenberg & Knowlton, 2014), greater vividness (Rubin, Burt & Fifield, 2003; Rubin, Schrauf & Greenberg, 2003), and important for forming mental representations of both past and imagined future events (Greenberg & Rubin, 2003). Imagery has also been identified as a component of autobiographical memory (Svoboda et al., 2006). Here, I define episodic memory as memory for a recently occurring event (on a scale of minutes/hours). Autobiographical memory is of memory of episodic events that have had a chance to be rehearsed and integrated into a personal schema (see Chapter 1 for further discussion of a distinction between them). A key area of interest is then whether mental imagery is a critical and necessary component within episodic and autobiographical memory.

Mental imagery and episodic memory have clear parallels; both consider the internal generation of a representation upon which a subjective experience can occur. A recollective experience is typically accompanied by mental imagery (Rubin et al., 2003) and future thinking too (Atance & O'Neill, 2001). Spatial theories of episodic memory, such as scene construction theory (Hassabis & Maguire, 2007; Maguire & Mullally, 2013), consider how recalled items are bound in 3D mental space and mentally represented. It suggests there is a relationship between internal representation using imagery based processes and event recollection.

Neuropsychological evidence from patient studies also suggests a close relationship between imagery and autobiographical remembering. In a disorder termed Severely Deficient Autobiographical Memory (SDAM), healthy adults with otherwise intact cognitive function report an inability to vividly recollect their past and show poor performance for the recovery of visual information (Palombo et al., 2015). Palombo and colleagues (2015) examined both neurological and behavioural outcomes of 3 individuals with SDAM who were otherwise completely healthy. They found evidence of impaired episodic retrieval for visual information and the absence of neural patterns of activity usually found during episodic recollection. Yet if a task could be completed without episodic processes their performance was no different to other adults. A possible explanation of these findings is a failure to bind visual information to a cue at retrieval, and thereby reducing the recollection of a rich and detailed experience.

At the other end of this spectrum are individuals with highly superior autobiographical memory (HSAM; LePort et al., 2012). These individuals demonstrate a better memory for details in their autobiographical memory which is accompanied by enhanced activity in related brain regions associated with memory representation compared to controls (Santangelo et al., 2018). Despite the exceptional ability for autobiographical details, in in tests of mental imagery ability they show no difference in performance to controls (LePort, Stark, McGaugh & Stark, 2017). It suggests that mental imagery may not be the contributing factor to producing rich and detailed recollections of autobiographical events observed in individuals with HSAM. Although, this piece of research assessed mental imagery by how efficiently they could combine images and interpret them. They asked participant to combine pairs of symbols and shapes (e.g. letter "D" rotated on its side combine with letter "J") and report the forms they could think of (e.g. umbrella). Arguably this test includes elements of mental imagery and rotation, but also imagination. It does not really assess the experience of picturing a mental image in the mind's eye without external sensory input in relation to memory performance. It further highlights the earlier point of the necessity for clarity when defining mental imagery.

The link between mental imagery and episodic memory seems to be centred on the experience of recollection and the visual details that can be recalled. The cases of both poor and superior autobiographical memory, and their limited respective findings of a relationship to visual imagery do point towards individual variation existing, and likely contributing, to the ability to produce vivid and rich mental representations. Therefore, gaining clarity on how individual differences in imagery can relate to our experience of episodic memory is a key area to examine.

4.1.3. Individual differences in imagery and episodic memory.

A condition termed 'aphantasia' describes a lack of mental imagery ability (Zeman et al., 2015). Whilst not a completely new phenomenon, aphantasia has attracted a renewed interest since Zeman et al. (2015) published and led to acknowledgement that mental imagery may not occur in every individual. In addition to the absence of visual imagery, those who report having aphantasia also report a reduction of imagery in other senses (Dawes, 2020). Interestingly, an individual may not even by aware their experience of mental imagery (or lack thereof) may differ to others (e.g. Clemens, 2018; Lawrence, 2020). Rising evidence emphasises that the use of mental imagery can vary between individuals and presents a need to understand how individual variation may relate other cognitive processes, including that of episodic memory.

Vividness ratings of past recollection provide a good indication that sensory-perceptual details of a generated scenario have been engaged with and relived (Wheeler, Petersen & Buckner, 2000). Research also suggests that the strength of recollection is associated with vividness (Rubin, 2005). The Vividness of Visual Imagery Questionnaire (VVIQ; Marks, 1973) is an established method of assessing individual ability to generate vivid visual imagery. Using the VVIQ, D'Argembeau and Van der Linden (2006) examined the relationship between individual variation and the phenomenological properties of both past autobiographical memory and imagined future events. They found individuals with higher visual imagery scores reported great visual details, more details from other sensory modalities, and clearer representation of both time and spatial information. However, the findings regarding vividness in episodic memory are inconsistent. In contrast, Greenberg and Knowlton (2014) did not find that scores on the VVIQ correlated with a sense of reliving, nor with visual imagery within memories.

One possible explanation of this inconsistency in findings related to memory research has been that mental imagery has been treated as an undifferentiated construct, rather than differentiating between spatial imagery and object imagery abilities separately (Aydin, 2018; Sheldon et al., 2016). Work that has examined memory performance and imagery constructs has demonstrated that spatial imagery ability and object imagery ability may contribute in different manners to memory. For example, Sheldon and colleagues (2016) suggest that it is spatial imagery ability that is critical for constructing an event in the mind, which is in line with spatial theories that propose a role of spatial processing to create a scaffold to build a memory on (e.g. Hassabis et al., 2007; Mullally & Maguire, 2013). They used dynamic visual noise (DVN) displayed at recognition to interfere with the availability of imagery processes during the task and compared performance to a control condition without the disruption. They found that spatial imagery ability predicted a negative effect of DVN for retrieving event details and spatial details, but not for feature details (e.g. colour, size). Overall, their findings advocate for the inclusion of individual differences when investigating memory. It suggests that individuals can rely differently on an imagery component in memory which in turn has consequences on the experience of remembering.

Focusing on object imagery, Vannucci, Pelagatti, Chiorri and Mazzoni (2016) examined the role of object imagery ability in memory. More specifically they assessed the impact of object imagery on number of autobiographical memories recalled, the ease of retrieval (as indicated by retrieval time), and phenomenological characteristics such as vividness. They found that individual who report high object imagery ability remember more autobiographical memories, with shorter retrieval times, and produced more sensory/perceptual details mainly recalled as visual images, compared to low object imagery ability. The high object imagery group also reported a greater number of remote involuntary autobiographical memories (those that come to mind spontaneously without conscious or deliberate attempt of retrieval). Overall, it suggests that object imagery may be directly relevant for feature details in memory. It also highlights a factor of age of memory; the consequences of imagery ability may be different depending on the time period the retrieval is generated from. This warrants further investigation to determine if the contribution of imagery varies as a result of the age of a memory.

Aydin (2018) has looked at the contribution of both object and spatial mental imagery for autobiographical and future thinking. They asked participants to generate two past events and two future events and write a detailed description for each, along with providing phenomenological ratings. Object imagery ability predicted several phenomenological ratings of past events including coherence, visual details, and emotional intensity. This was expected in line with object imagery being related to generating vivid sensory perceptual details. For future thinking, object imagery was only related to emotional intensity. On the other hand, spatial imagery ability was related to episodic specificity for both past and future thinking. Similar to Sheldon et al. (2016), spatial imagery ability appears to be related to event details.

In sum, evidence suggests that mental imagery needs to be consider in separate sub-systems of spatial imagery and object imagery. Individual ability in both appear to contribute to different elements during memory retrieval and the recollection experience depending on the processes they require. Object imagery seems to contribute to sensory perceptual aspect of past thinking and spatial imagery for the construction of the event in an internal space with detailed information.

4.1.4. Chapter aims.

In this chapter I take an individual differences approach to examine how visual mental imagery is related to episodic memory. The mixed findings of the impact of mental imagery, and the parallels between spatial theories of episodic memory and mental imagery demonstrate that mental imagery does need to be considered in the examination of episodic memory as a whole. Without acknowledging what impact individual imagery ability has on a range of memory processes, we cannot have a full picture of how a vivid reliving experience occurs in episodic memory. Additionally, mental imagery needs to be treated as more than a unitary construct to fully understand how different types of imagery contribute.

The aim of this chapter is to explore the relationship between visual mental imagery and both episodic and autobiographical memory. Episodic memory refers to a shorter event memory system for reliving sensory experience whereas autobiographical memory refers to events from a longer time period that have had the opportunity to be rehearsed and built into a personal schema (for further details see Chapter 1). I examine the contribution of imagery as two structures of imagery spatial and object imagery in order to overcome the limitations of examining imagery as a unitary construct. Experiment 1 examines the contribution of spatial and object imagery to autobiographical memories from a recent time period as well as older memories to determine the contribution of imagery over different time points. Experiment 2 looks at the relationship between imagery and a lab-based scene recognition task to explore the relationship in an episodic memory recognition task containing both objective and subjective measures.

4.2. Experiment 1

Previous research has demonstrated differences in the contribution of spatial and object imagery for past and future autobiographical thinking (see Aydin, 2018). Yet whether this contribution is stable over time for autobiographical memory remains to be investigated. Therefore, the main objective for this experiment was to establish how imagery constructs of spatial and object imagery contribute to both recent and remote autobiographical memory. Using a within-subjects design of recounting both recent (defined as in the past two weeks) and remote (defined as approximately ten years ago) autobiographical events, participants provided descriptions and phenomenological ratings. They also completed the OSIQ (Object and Spatial Imagery Questionnaire; Blajenkova et al., 2006) as a measure of object and spatial imagery ability. Object imagery has been suggested to relate to reflective processes, whereas spatial imagery is more related to retrieval of event details (Aydin, 2018). I examine both the phenomenological characteristics and episodic specificity of recent and remote events. If the contribution of each imagery construct is consistent over time, then I expect to find similar results in recent and remote memories.

A secondary aim was to explore how imagery measures of spatial and object imagery relate to other imagery measures focusing on vividness. Individual differences of vividness imagery ability were measured by the Vividness of Object and Spatial Imagery Questionnaire (VOSI; Blazhenkova, 2016) which is a self-report measure that considers the separate constructs of visual imagery (spatial and object) in regard to how vivid the mental images are. Similarly, the Vividness of Visual Imagery Questionnaire (VVIQ; Marks, 1973) is a common measure of overall vividness in mental imagery however it does not differentiate between spatial and object imagery. If the self-report imagery scores for each imagery dimension were correlated with vividness within that dimension it would suggest that vividness and general ability within that dimension were related. It was predicted that OSIQ spatial and VOSI spatial imagery scores would correlate. Similarly, it was expected OSIQ object and VOSI object imagery scores would also be related. I expected that VVIQ scores would be correlated with both VOSI object and spatial scores as it represented a unitary construct of imagery.

4.2.1. Experiment 1 Method.

4.2.1.1. Participants.

A total of 48 participants were recruited (13 male) with an age range of 18 to 61 (Mean = 29.9, SD = 13.18). Participants completed the questionnaire either at home on a personal computer or were invited to attend a lab session and use a computer in a quiet booth. Participants were recruited from the University of East Anglia and the surrounding area via paid participant panel scheme and offered the chance to win a voucher for their time through entry into a prize draw. If the participants were psychology undergraduates of the University East Anglia, they were offered course credit for their participation instead.

4.2.1.2. Imagery Measures.

The OSIQ (Object and Spatial Imagery Questionnaire; Blajenkova et al., 2006; see Appendix E) is a self-report measure that assesses individual differences in visual imagery for spatial and object imagery separately. There are 15 questions assessing object visualisation (e.g. "My images are very colourful and bright") and 15 questions assessing spatial visualisation (e.g. "I can easily imagine and mentally rotate 3D geometric figures"). Vividness is not specifically measured; however some questions do refer to how vivid an experience is (e.g. "My images are very vivid and photographic" within the object imagery measure). Each of the 30 statements were rated on a five-point scale from 1 (strongly disagree) to 5 (strongly agree). A score for object imagery and spatial imagery was generated separately by calculating the average for the corresponding ratings.

The VOSI (Vividness of Object and Spatial Imagery Questionnaire; Blazhenkova, 2016; see Appendix F) measures vividness of spatial and object imagery. There are 14 items for the vividness of object imagery dimension (e.g. "appearance of a candle fire") and 14 items for the vividness of spatial imagery dimension (e.g. "locations of your house on a map of the city"). Participants are asked to imagine items and rate how vivid their mental imagery is on a five-point scale: "no image at all, you only know you are thinking of the object", "vague and dim", "moderately clear and vivid", "clear and reasonable vivid", "perfectly clear and as vivid as normal vision". Higher scores are indicative of higher vividness in each dimension.

VVIQ (The Vividness of Visual Imagery Questionnaire; Marks, 1973; see Appendix A) is a very common measure of an individual's ability to generate vivid visual mental imagery. The VVIQ is a 16 item questionnaire that asks participants to rate the vivid of their mental image for each item and has the same five-point rating scale as used in the VOSI outlined above. The traditional coding of the VVIQ is 1 point for vivid imagery and 5 points for no generation of a mental image. Here we reverse the scoring to mean that high scores equate to higher visual imagery in order to have consistency in direction of the scales across the questionnaires.

4.2.1.3. Procedure.

For participants who were tested in the lab, participants were tested in small groups (maximum of six) in individual testing booths. Participants opted to take part in the online version of the study were sent a link to complete the questionnaire. Both groups of participants received the same online questionnaire to complete delivered via Qualtrics.

In the event memory section, participants generated a total of four autobiographical events: two from the past two weeks, and two from approximately ten years ago. Participants were first given an overview of what constituted as ‘an event’. They were told it must be an event they were personally involved in, that they actually ‘remember’ they were present rather than ‘know’, and that occurred a specific time and place. Following the general event instructions, shorter prompts were displayed with a box to write their memory in. They were given the time period their event must be from (around 10 years ago or from the past 2 weeks). They were instructed to remember the event in as much detail as possible to mentally re-experience it. Additionally, they were advised to think about where and when it happened, sensory details such as colours/sounds/smells/physically sensations, and what they were thinking/feeling at the time. Following the generation and write up of an event, they were asked to provide some ratings about the memory. The ratings were items adapted from the Memory Characteristics Questionnaire (MCQ; Johnson et al., 1988) and the Autobiographical Memory Questionnaire (AMQ; Rubin et al., 2003; Butler, Rice, Wooldridge & Rubin, 2016). See Appendix G.

In the imagery section participants completed the three imagery questionnaires. The presentation order of either imagery questionnaires or memory recollection was randomised. Additionally, the order of recent and remote memory questions within the memory recollection block was also randomised. The completion of the whole questionnaire took approximately 1 hour.

4.2.1.4. Coding.

The event descriptions were coded based on scheme previously used by Levine et al. (2002) to examine episodic specificity. For each written memory, the central event was defined; if more than one event was present, the one with the most detail was used. Once the central event was decided, the event was segmented into internal and external details. Internal details were episodic information related to the content of the event being described, such as thoughts, location, perceptual details. External details were information that was non-episodic that were external to the event being described or repetition of information, for example "I still like ice cream". Each unique detail was scored 1 point and were added together to provide scores for the amount of internal and external details for each event.

4.2.2. Experiment 1 Results.

4.2.2.1. Visual imagery measures.

The correlations between the imagery measures were calculated to determine how the imagery questionnaires may relate to one another. See *Table 4.1.* for means and standard deviations of imagery measures as well as correlations between them. OSIQ scores for spatial and object imagery were calculated based on established procedures by averaging scores for each dimension (Blajenkova et al., 2006). The mean score for object imagery was 3.39 (SD = 0.61), and the mean score for spatial imagery was 2.72 (SD = 0.59). For VOSI scores, the mean score for vividness of object imagery was 52.85 (SD = 7.64), and the mean score for vividness of spatial imagery was 43.38 (SD = 11.2).

Correlational analyses showed there was no correlation between OSIQ spatial and OSIQ object imagery scores supporting the distinction that these measure two separate constructs that are unrelated (see *Figure 4.2.*). Critically, as they are not correlated, they can be used as acceptable predictors in the regression model. OSIQ object scores were significantly correlated with VOSI object scores suggesting higher object imagery is related to high vividness of object imagery. OSIQ spatial imagery was significantly correlated with VOSI spatial imagery scores but not with VOSI object imagery. Scores of the VOSI scale were related to each other: VOSI object and VOSI spatial scores showed a significant positive correlation (see *Figure 4.3.*). It suggests that object and spatial imagery may not be completely divisible into separate and unrelated constructs when considering the vividness of each dimension. Scores on VVIQ were positively correlated both with VOSI object and VOSI spatial scores (see *Figure 4.4.*). VVIQ was correlated with OSIQ object imagery, but not with OSIQ spatial imagery (see *Figure 4.5.*).

Table 4.1. Means (M), standard deviations (SD), and correlations between the imagery measures.

	M	**SD**	**OSIQ-Object**	**OSIQ-Spatial**	**VOSI-Object**	**VOSI-Spatial**	**VVIQ**
OSIQ-Object	3.39	0.61	-	-	-	-	-
OSIQ-Spatial	2.72	0.59	-0.2	-	-	-	-
VOSI-Object	52.85	7.64	0.5***	-0.02	-	-	-
VOSI-Spatial	43.48	11.2	0.32*	0.47**	0.6***	-	-
VVIQ	61.9	8.85	0.46**	0.04	0.71***	0.45**	-

* *p* < .05
** *p* < .01
*** *p* < .001

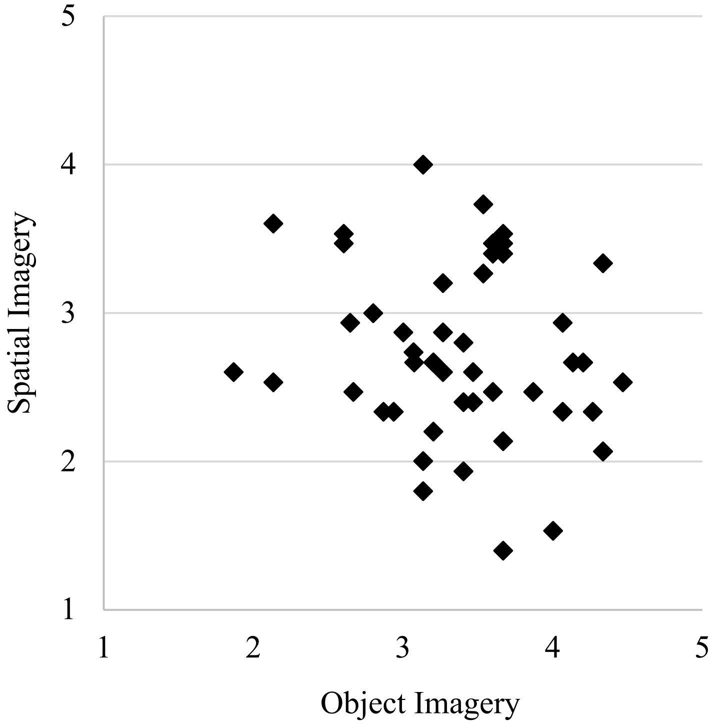

Figure 4.2. Scatterplot displaying the average OSIQ scores for object and spatial imagery dimensions.

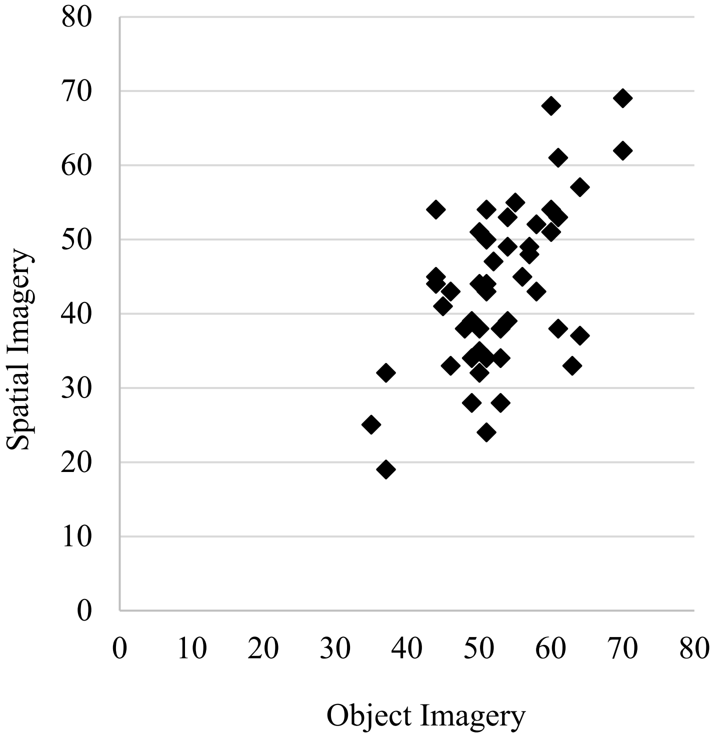

Figure 4.3. Scatterplot displaying correlation of scores on the VOSI questionnaire for vividness of object and spatial imagery.

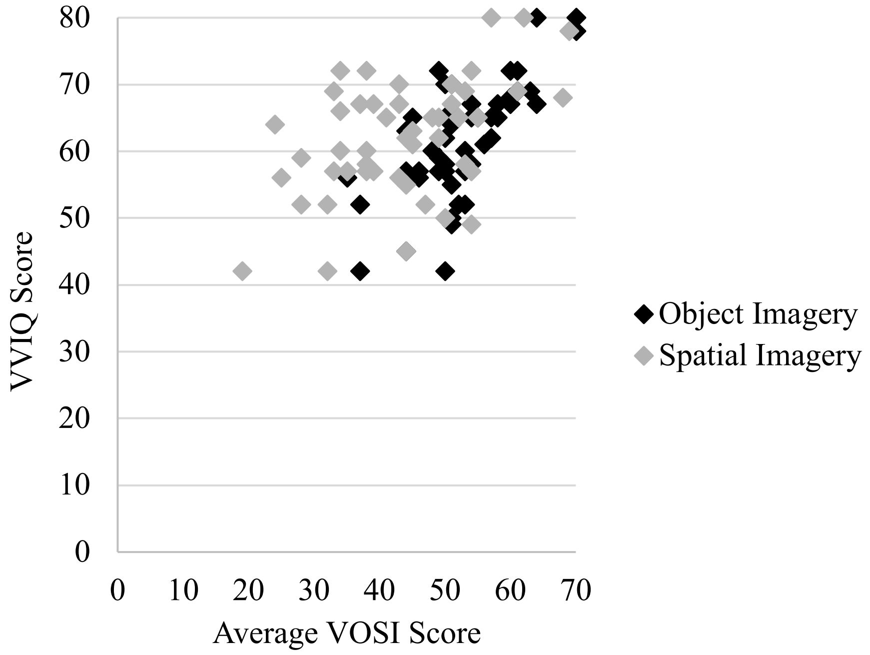

Figure 4.4. Scatterplot displaying the scores for VVIQ and VOSI questionnaires. VVIQ scores correlate with both scores on VOSI object and spatial imagery.

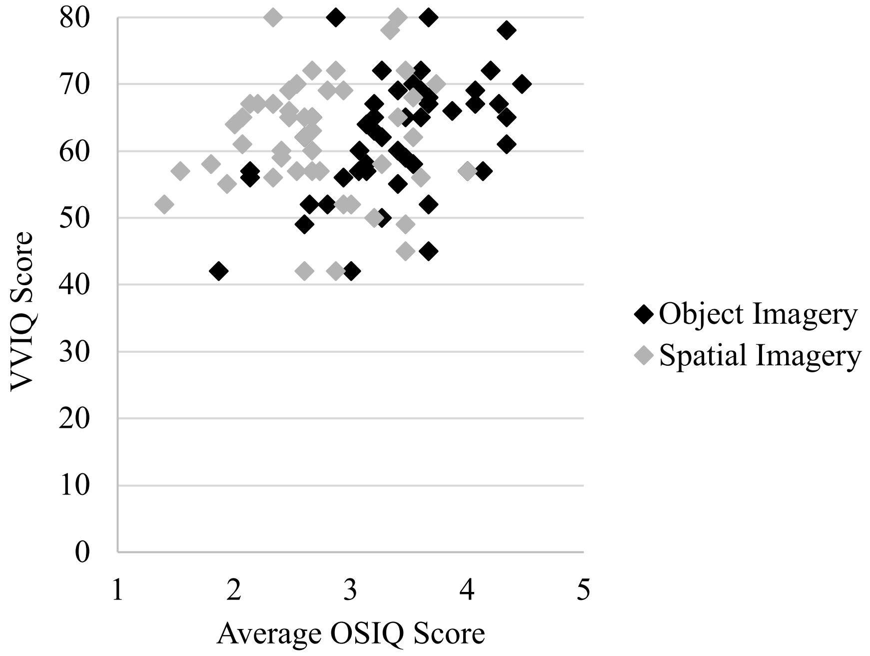

Figure 4.5. Scatterplot of average scores on OSIQ and VVIQ scores, split for both object imagery and spatial imagery. The plot shows OSIQ object imagery ability is correlated with VVIQ score, whereas OSIQ spatial imagery ability is not correlated with VVIQ score.

4.2.2.2. Visual imagery and phenomenology of recent and remote AM.

The means and standard deviations for the phenomenological ratings for recent and remote memories are shown in *Table 4.2*. As in previous literature, the ratings for both recent memories and remote memories were averaged to produce one value for each phenomenological ratings of recent and remote conditions (see Aydin, 2018; D'Argembeau & Van der Linden, 2006; Wang et al., 2011). Ratings of recent autobiographical memories were significantly higher than remote autobiographical memories in all phenomenological characteristics apart from rehearsal.

To evaluate the influence of object and spatial imagery scores on the phenomenological ratings of recent and remote memories, multivariate multiple regression analyses were carried out. The same regression approach as Aydin (2018) using OSIQ scores was conducted; this was to establish individual differences in the constructs of mental imagery ability rather than only vividness ability. The independent variables were the OSIQ object and OSIQ spatial imagery scores (average response to object and spatial items respectively). The dependent variables were the subjective ratings about the memories. See *Table 4.3*. for standardised beta weights and R^2 values.

For recent memory, object imagery significantly predicts the experience of reliving (b = 1.14, $t(45)$ = 4.37, p < .000, 95% CI [0.62, 1.67]; model Cohen's f^2 = 0.43), the feeling experienced (feelings/emotion/atmosphere) (b = 0.72, $t(45)$ = 2.44, p = .019, 95% CI [-0.13, 1.08]; model Cohen's f^2 = 0.14), the presence of visual details (b = 0.72, $t(45)$ = 4.64, p < .001, 95% CI [0.41, 1.03]; model Cohen's f^2 = 0.52), the presence of imagery (visualisation in mind's eye) (b = 0.74, $t(45)$ = 4.42, p < .000 , 95% CI [0.40, 1.08]; model Cohen's f^2 = 0.43), and the ability to recall the layout of the setting (b = 0.83, $t(45)$ =3.24, p = .002, 95% CI [0.32, 1.35]; model Cohen's f^2 = 0.30). Although spatial imagery scores predicted coherence and layout, this did not remain the case after adjusting for multiple comparisons (corrected alpha 0.025).

Table 4.2. Means (M) and standard deviations (SD) of the phenomenological ratings for recent and remote autobiographical memories.

	Recent		**Remote**				
	M	**SD**	**M**	**SD**		**t**	**Brief Description**
Reliving	5.75	1.25	4.30	1.69		7.24**	While remembering the event, I feel as if I am reliving/experiencing it.
Time Travel	5.55	1.23	4.33	1.75		6.26**	As I remember the event, I feel that I travel back to the time when it happened, that I am a participant in it again, rather than an outside observer tied to the present.
Feeling	5.28	1.26	3.92	1.75		6.42**	While remembering, it is as if I am experiencing the same feelings, emotions, and/or atmosphere again.
Visual Details	6.32	0.75	5.21	1.61		5.30**	My memory for this event involves visual details.
Auditory Details	4.65	1.77	3.49	1.53		5.17**	My memory for this event involves sounds.
Coherence	5.79	1.29	4.26	1.86		7.21**	As I remember the event, it comes to me in words or in pictures as a coherent story or episode and not as an isolated face, observation, or scene.
Imagery	5.80	0.80	4.54	1.62		6.31**	As I remember, I experience a mental image of the event in my mind's eye.
Words	3.53	2.11	3.03	1.78		2.51*	As I remember the event it comes to me in words.
Layout	6.05	1.16	4.73	1.63		6.07**	While remembering, I experience a scene in which the elements of the setting are located relative to each other in space.
Belief	6.73	0.47	5.47	1.59		6.08**	I believe the event occurred in the way I remember it and that I have not imagined or fabricated anything that did not occur.
Valence	5.21	1.28	4.63	1.64		2.02*	How positive or negative is this memory?
Rehearsal	3.81	1.50	3.55	1.57		1.03	Since the event happened, I have thought and/or talked about this event.
Perspective	1.15	0.41	1.54	0.8		-	When you think about this memory, do you see it as if through your own eyes (1st person) or as an observer to the event (3rd person)?

NB: degrees of freedom 47 in all cases. All ratings were on a scale of 1 to 7, with 7 representing a higher score, apart from perspective which was categorical either 1st or 3rd person.
* $p < .05$
**$p < .001$

For remote memory, object imagery significantly predicts the experience of reliving ($b = 1.19$, $t(45) = 3.09$, $p = .003$, 95% CI [0.42, 1.97]; model Cohen's $f^2 = 0.22$), the experience of mental time travel ($b = 1.05$, $t(45) = 2.55$, $p = .014$, 95% CI [0.22, 1.87]; model Cohen's $f^2 = 0.15$), the feeling (feelings/emotion/atmosphere) ($b = 1.18$, $t(45) = 2.95$, $p = .005$, 95% CI [0.37, 1.98]; model Cohen's $f^2 = 0.2$), the presence of visual details ($b = 1.24$, $t(45) = 3.44$, $p = .001$, 95% CI [0.51, 1.97]; model Cohen's $f^2 = 0.27$), the imagery (visualisation in mind's eye) ($b = 1.50$, $t(45) = 4.41$, $p < .001$, 95% CI [0.82, 2.19]; model Cohen's $f^2 = 0.43$), the belief ($b = 1.08$, $t(45) =2.98$, $p = .005$, 95% CI [0.35, 1.81]; model Cohen's $f^2 = 0.2$), and rehearsal ($b = 0.94$, $t(45) =3.24$, $p = .013$, 95% CI [.21, 1.68]; model Cohen's $f^2 = 0.15$). Spatial imagery scores predicted layout but this finding was not retained after correction for multiple comparisons.

Table 4.3. Multiple regression analyses of the phenomenological ratings for recent and remote autobiographical memory with object and spatial imagery measures.

	Recent			**Remote**		
	R^2	**Standardised ß**		**R^2**	**Standardised ß**	
		OSIQ object	**OSIQ spatial**		**OSIQ object**	**OSIQ spatial**
Reliving	0.30	1.14*	0.29	0.18	1.19*	0.17
Time Travel	0.05	0.48	0.13	0.13	1.05*	0.42
Feeling	0.12	0.72*	0.40	0.17	1.18*	-0.07
Visual Details	0.34	0.72*	0.32	0.21	1.24*	0.33
Auditory Details	0.01	0.24	0.09	0.07	0.62	-0.21
Coherence	0.12	0.50	0.69	0.04	0.52	0.46
Imagery	0.30	0.74*	0.16	0.30	1.50*	0.42
Words	0.05	0.37	0.79	0.06	0.08	0.75
Layout	0.23	0.83*	0.59	0.13	0.74	0.81
Belief	0.04	0.16	0.02	0.17	1.08*	-0.07
Valence	0.14	0.46	-0.59	0.04	0.39	0.52
Rehearsal	0.00	-0.02	0.11	0.13	0.94*	0.41
Perspective	0.03	0.12	0.00	0.02	0.19	0.11

NB: numbers to 2 decimal places.

---

* $p < .025$; p-value adjusted for multiple comparisons with Bonferroni correction.

4.2.2.3. Visual imagery and the specificity of recent and remote AM.

To evaluate the influence of object and spatial imagery scores on the number of internal details and external details within recent and remote memories, multivariate multiple regression analyses were carried out. The independent variables were the OSIQ object and OSIQ spatial imagery scores (average response to object and spatial items respectively). The dependent variables were the total number of internal and external details averaged across the 2 events for the remote event memories, and for the recent event memories. See Table 4.4. for standardised beta weights and R^2 values.

For remote memories, the mean number of internal details was 11.59 (SD = 4.54) and for external details was 2.42 (SD = 1.74). For recent memories, the mean number of internal details was 12.36 (SD = 4.11) and for external details was 2.17 (SD = 1.52). Neither object imagery or spatial imagery predicted the number of details, either internal or external. This was the case for both recent autobiographical and remote autobiographical memory (see Table 4.5.).

Table 4.4. Multiple regression analyses of the internal and external details for recent and remote autobiographical memory with object and spatial imagery measures.

	Recent			**Remote**		
	R^2	**Standardised ß**		**R^2**	**Standardised ß**	
		OSIQ object	**OSIQ spatial**		**OSIQ object**	**OSIQ spatial**
Internal details	0.014	0.798	-0.052	0.001	-0.22	-0.028
External details	0.031	-0.213	-0.442	0.018	-0.124	-0.399

NB: numbers to 3 decimal places.

Table 4.5. The t and p values, plus 95% Confidence Intervals (CI), for the multivariant regression analyses of internal and external details of recent and remote memories with object and spatial imagery scores as predictors.

	Recent			**Remote**		
	t	p	95% CI	t	p	95% CI
Internal						
Object	0.78	.440	[-1.23, 2.86]	-0.19	.848	[-2.52, 2.08]
Spatial	-0.05	.961	[-2.18, 2.08]	-0.02	.941	[-2.40, 2.34]
External						
Object	-0.57	.574	[-0.97, 0.54]	-0.29	.776	[-0.99, 0.75]
Spatial	-1.14	.260	[-1.22, 0.34]	-0.90	.365	[-1.30, 0.45]

4.2.3. Experiment 1 Discussion

This experiment looked at how difference imagery constructs contributed to memory processes of both recent (2 weeks) autobiographical events and more remote (10 years) autobiographical events. In both recent and remote events, object imagery ability but not spatial imagery ability was correlated with several phenomenological characteristics. For recent events that had occurred within the past two weeks, object imagery ability predicted the experience of reliving, the feelings associated with the original event, the presence of visual detail, generation of imagery of the event, and layout. For remote events that occurred approximately 10 years ago, object imagery ability predicted experience of reliving, the feelings associated with the original event, the presence of visual detail, generation of imagery of the event, experiencing mental time travel, belief and rehearsal. There was no relationship between object imagery and spatial imagery with episodic specificity of both internal and external details for either memory periods.

The finding that object imagery ability predicts the presence of visual detail and imagery in both recent and remote events is consistent with the idea that object imagery is associated with generating vivid mental images involving sensory-perceptual details such as shape or colour of objects (Blajenkova et al., 2006; Vannuci et al., 2016). For remote events, there was a medium effect of the model whereas for recent events, the effect was large (for effect size levels see Cohen, 1998). There was also a greater rating for the presence of visual details for recent events compared to remote events, suggesting that the visual details vary over the age of an event memory. Previous research has suggested that remote events are rated lower in imagery than more recent events (e.g., D'Argembeau & Van der Linden, 2006; Szpunar & McDermott, 2008). In this experiment we found there was a significantly lower ratings on imagery (defined as the presence of mental imagery in the mind's eye) for remote compared to recent events. However, despite this object imagery ability predicted the presence of imagery in both recent and remote events, with a large effect in both models. Furthermore, the experience of reliving and experiencing the same feeling as at the original event were also related to object imagery ability for both recent and remote events, supporting a link between mental imagery and a sense of reliving (Greenberg & Knowlton, 2014; Irish, Lawlor, O'Mara & Coen, 2011; Rubin, Schrauf & Greenberg, 2003).

Interestingly, mental time travel of going back and projecting the self in subjective time was only predicted by object imagery ability in remote memories. Similarly, rehearsal and belief were correlated with object imagery ability for remote but not recent memories. One possibility is that object imagery is more important for these aspects for recalling temporally remote events than more temporally recent events. Further investigation is needed to confirm this hypothesis.

Unlike Aydin (2018) this experiment did not find object imagery ability predicted coherence of autobiographical memory. Coherence refers to how the memory unfolds over time, occurring as a continuous sequence or episode rather than isolated scenes. Here we found that it was spatial imagery ability linked to coherence in recent events, although this did not remain a significant predictor after correction for multiple comparisons. This is more in line with the findings by Sheldon et al. (2016) who determined it was spatial imagery that related to how events unfolded over time. Another perhaps surprising finding was that spatial imagery did not predict recall of event layout which pertained to the remembering the setting and the location of elements relative to one another. For both recent and remote events spatial imagery ability was not related following correction for multiple comparisons. It is possible that due to the sample size there was not enough power to detect this effect. Alternatively, reflecting on the layout of a recall event may not engage imagery processes.

Looking at the imagery measures, similar to Aydin (2018) no correlation was found between the OSIQ object and spatial imagery scores adding further support that this questionnaire measures separate constructs. However, unlike the findings by Aydin (2018), the VVIQ scores correlated to OSIQ object imagery but not spatial imagery rather than both. The VVIQ has received criticism over not differentiating between imagery constructs and measuring both vividness of object and spatial imagery. In this experiment VVIQ related to only one imagery construct (object imagery), but it did relate to both vividness of object imagery and vividness of spatial imagery in the VOSI. Overall, it suggests that vividness may be harder to measure and quantify in terms of a separate imagery construct.

Unlike Aydin (2018), we did not find that spatial imagery contributed to the specificity of autobiographical events as indexed by the coding of internal and external memory details. There were a large number of internal details recalled in our experiment, which may be a result of giving specific instructions to consider perceptual aspects and details such as what they were thinking. This may have created some bias as to what participants focused on during the recall. Additionally, we must also consider that we only collected two detailed memories from each time period. A larger number of memories may have given a better overview of details to create a more meaningful average.

In conclusion, this experiment has demonstrated object imagery ability contributes to both recent and remote autobiographical memory processes. It has highlighted that object imagery is predictive of sensory-perceptual aspects of both recent and remote memories including the experience of reliving, the presence of visual details, and visualisation of imagery. Further, it has demonstrated that imagery contributes differently depending on the age of an autobiographical memory. Object imagery ability is additionally predictive of belief, rehearsal, and mental time travel in older memories. It suggests individual difference in imagery ability have greater consequences depending on the age of a memory that is being examined.

4.3. Experiment 2

In an additional experiment, we invited participants from experiment 1 who came to a lab session to complete the questionnaire to remain in the lab and complete a memory recognition task. The aim of this task was to assess if an individual's spatial imagery ability and performance in a lab-based scene recognition task at modulated perspectives were related. Mental imagery can involve the inspection and manipulation of material held in the mind's eye (Cumming & Eave, 2018). In memory tasks, participants are often asked to recall previous events either in full or recall specific details and orientations. Yet consideration for individual differences in imagery ability is often overlooked.

Object imagery has been linked to sensory and perceptual elements of an event (Aydin, 2018; Vannuci et al., 2016). Spatial imagery has been linked to the relational layout in context space (Aydin, 2018; Sheldon et al., 2016). In the present experiment we present two highly similar mountain scenes to first be learnt and then recognised. At recognition we present the same two scenes but at varying degrees of rotation. Testing recognition by using the scenes at manipulated angles would require not only being able to recognise the original mountain range scene, but also to mentally rotate it to match the shown viewing perspective. We examine the relationship spatial and object mental imagery has separately on the accuracy, reaction time and confidence on the task. Assessing these relationships, we can determine relationships between imagery and objective/subjective measures of memory tasks.

If spatial imagery ability is related to ease of completing a spatial manipulation task, I expected a significant relationship between accuracy and self-reported spatial imagery ability. Additionally, if imagery ability makes the task easier, I expected a relationship between reaction times and spatial imagery ability, with faster times associated with higher spatial imagery ability. Finally, if a stronger spatial ability has is related to the subjective judgements within a task, I expected an association between spatial imagery ability and confidence judgments. As this is a scene manipulation task and not related to sensory or perceptual elements, I did not predict any relationship of accuracy, reaction time, or confidence with the self-reported scores of object imagery ability.

4.3.1. Experiment 2 Method

4.3.1.1. Participants.

Twenty participants from the University of East Anglia who completed Experiment 1 within the lab remained to complete the task for additional course credit through a research participation scheme. Three participants were removed from the final set: one due to non-responses in over half of trials, and the other two due to very poor task performance suggestive of task misunderstanding (only 1% and 8% of trials correct). The final sample comprised of seventeen participants with an age range of 18 to 29 (2 males; Mean age = 20.24; SD age = 3.19).

4.3.1.2. Materials.

The stimuli were 40 still images comprised from two computer generated mountain ranges. Each range had 20 images taken as the mountain range was rotated around a vertical axis. Images were presented at a size of 640 by 480 pixels. Participant responses from the OSIQ (see Experiment 1: materials above) were used as the measure of individual object imagery and spatial imagery.

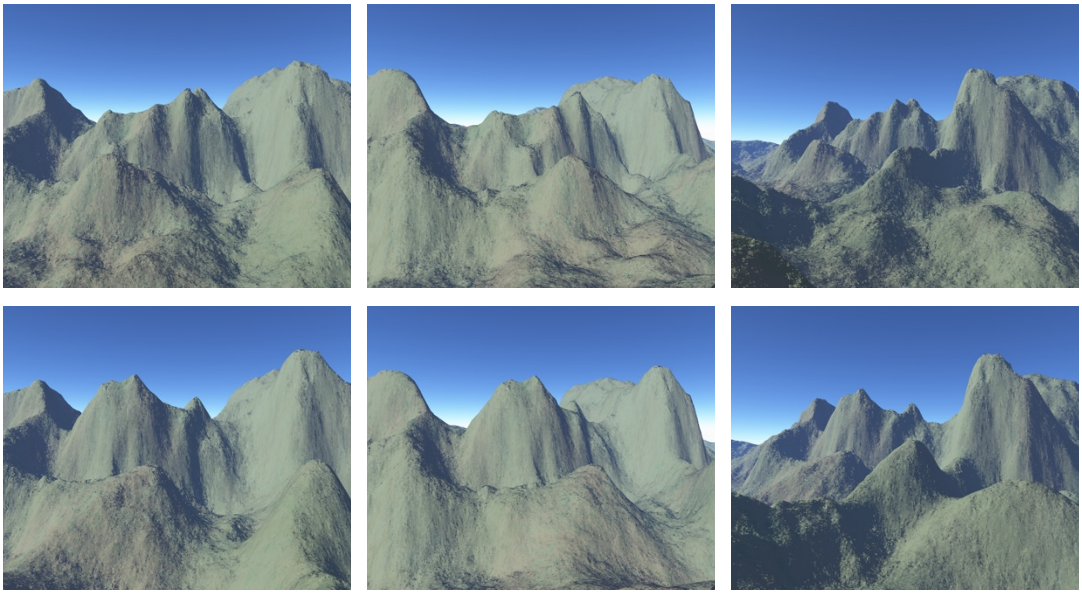

Figure 4.6. Examples of the mountain range stimuli. The top row shows one mountain range, rotated at various angles, and the bottom row shows a second mountain range, also rotated at various angles.

4.2.1.3. Procedure.

Participants were given the instructions verbally for all parts of the study at the start of the experiment. A summary of instructions was also displayed to participants at each stage as a reminder and an opportunity to ask questions. The experiment was presented using OpenSesame (Mathôt, Schreij & Theeuwes, 2012), an open-source presentation software, on a standard monitor and responses were made using a standard keyboard.

First, they learnt the correct response associated with each mountain scene image. A white fixation dot on a black background was presented for 2000ms and then one of the mountain scene images was displayed. Whilst the image was on screen, participants pressed either the ‘m’ or ‘n’ key, or the trial timed out after 2500ms. If they selected the correct response the following fixation crossed remained white. If they picked the wrong key press, the fixation cross presented was red for 300ms providing feedback the response was wrong. Each mountain scene was displayed for a total of 20 times to ensure participants could identify each scene. Participants were given their total accuracy and average response time for the task at the end of the 40 trials.

Next participants completed the experimental task. They were informed the images were still the same two mountain scenes from different viewpoints and their task was to correctly identify the mountain range being displayed using the ‘m’ and ‘n’ keys. They were also asked to provide a confidence rating of their belief in the accuracy of their response on a scale of one to five, with one being low and five being high. Explicit instructions to respond as quickly and as accurately as possible, as well as to use the full range of the confidence scale, were given to each participant before starting the task (see *Figure 4.7.*).

Participants completed a practice run beforehand. The practice task was a shortened version of the main experimental task and consisted of 40 trials displaying the original images once and 19 scenes of each mountain range at rotated angles. Once participants completed the practice task, they then completed a total of 240 trials presented in 3 blocks of 80 trials. Participants were able to take a short comfort break between blocks if needed. In each block the original scene and 19 rotations of both mountain ranges were presented twice in a pseudo-randomised order; the same image was never presented twice in a row.

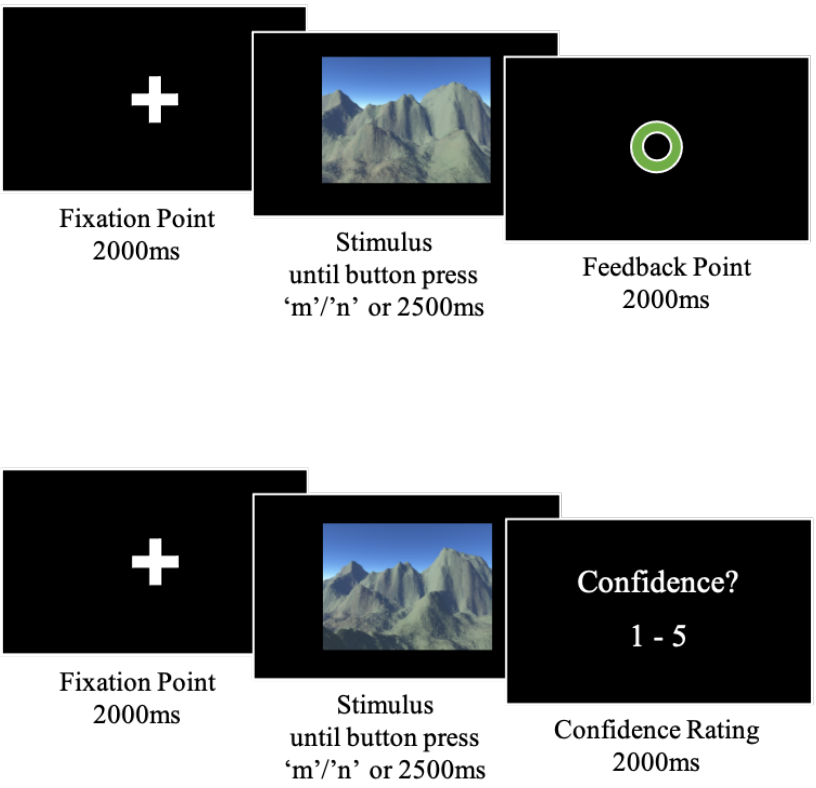

Figure 4.7. The top panel shows a trial for the training phase. Participants learn which mountain range corresponds to the keys 'm' and 'n'. This example is a shows an 'incorrect' feedback. The second panel shows a recognition trial. This example shows the same mountain range as above with the angle rotated, followed by a confidence indicator question.

4.3.2. Experiment 2 Results

4.3.2.1. Summary Statistics.

For the self-report measures of object and spatial imagery, the mean score for object imagery was 3.30 (SD = 0.56) and for spatial imagery was 2.65 (SD = 0.65). Response times, accuracy, and confidence measures were calculated. Overall mean correct response time was 929.91ms (SD = 230.75; range = 483.10 to 1376.55) which represented the response latency from the point of stimulus onset. For incorrect responses the mean response time was 935.33ms (SD = 249.92; range =

497.28 to 1407.43). For confidence of correct responses, the average confidence response was 2.94 (SD = 1). For incorrect responses the average was similar (M = 2.81; SD = 0.9).

Overall mean accuracy collapsed across all three blocks was 59% (SD = 0.16; range =18 – 90%). For the first block, mean accuracy was 60.06% (SD = 0.13; range = 38 – 78%), which remained similar in the second block (M = 58.2%; SD = 0.18; range = 13 – 96%), and the third block (M = 59.88%; SD = 0.2; range = 6 – 95%).

4.3.2.2. Correlations.

A series of correlational analyses were performed in order to determine if task performance measures were related to imagery styles. Uncorrected results are reported with a significance threshold of 0.05. In order to control for multiple comparison testing, we also conducted Benjamini-Hochberg adjustment with a false discovery rate of 0.1 (see Benjamini & Hochberg, 1995) and report where significance holds after correction.

First the correlation between the two imagery styles was assessed to determine the two constructs were not related. Self-report scores of object imagery and spatial imagery were not correlated ($r(15) = -.219, p = .399$). Based on previous literature suggesting a relationship between accuracy and confidence, we assessed association between accuracy and average confidence ratings. There was a significant moderate positive correlation between accuracy and confidence of correct response ($r(15) = .550, p = .022$). For accuracy and confidence response on incorrect trials there was a similar trend but this was not significant ($r(15) = .443, p = .075$).

Next correlations were tested between objective performance measures of mean accuracy and mean reaction times with each imagery style. Performance accuracy did not correlate with spatial imagery style ($r(15) = .332, p = .193$), or with object imagery style ($r(15) = -.115, p = .660$). There were also no association between mean reaction time for correct responses with spatial imagery ($r(15) = .247, p = .339$), nor object imagery ($r(15) = .100, p = .702$).

Finally, correlations between mean confidence scores and imagery styles were conducted. There was a significant moderate positive correlation between average confidence on correct trials and spatial imagery scores (*r*(15) = .637, *p* = .006) which remained significant after Benjamini-Hochberg correction. There was no correlation between correct confidence trials and object imagery scores (*r*(15) = -.067, *p* = .797). Average confidence for incorrect responses was associated with spatial imagery scores (*r*(15) = .576, *p* =. 015), and remained so following correction, but not with object imagery (*r*(15) = .011, *p* =. 968).

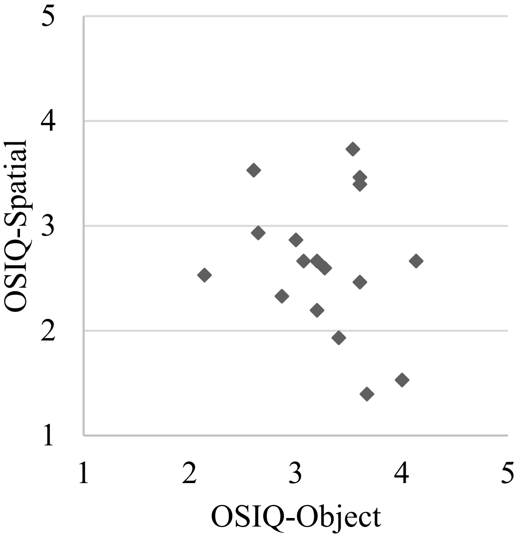

Figure 4.8. Scatterplot showing no significant relationship between scores on the OSIQ object and spatial imagery dimensions.

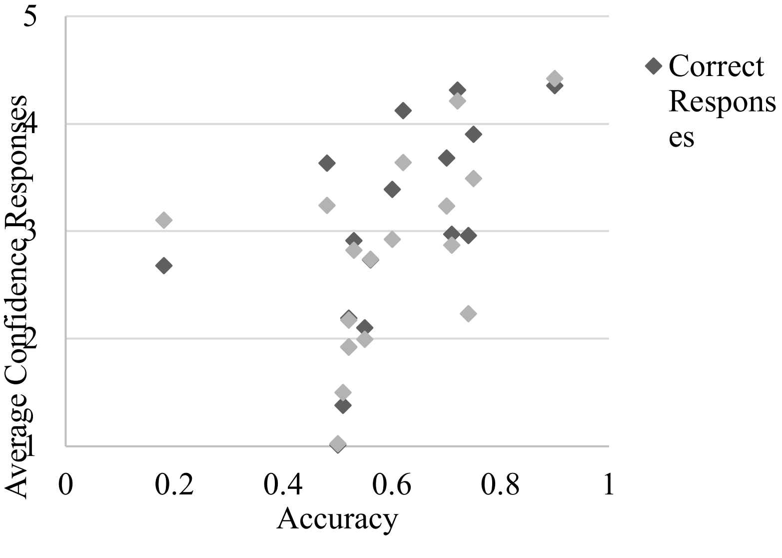

Figure 4.9. Scatterplot showing the relationship between accuracy, measuring as a proportion of correct responses, to average confidence ratings.

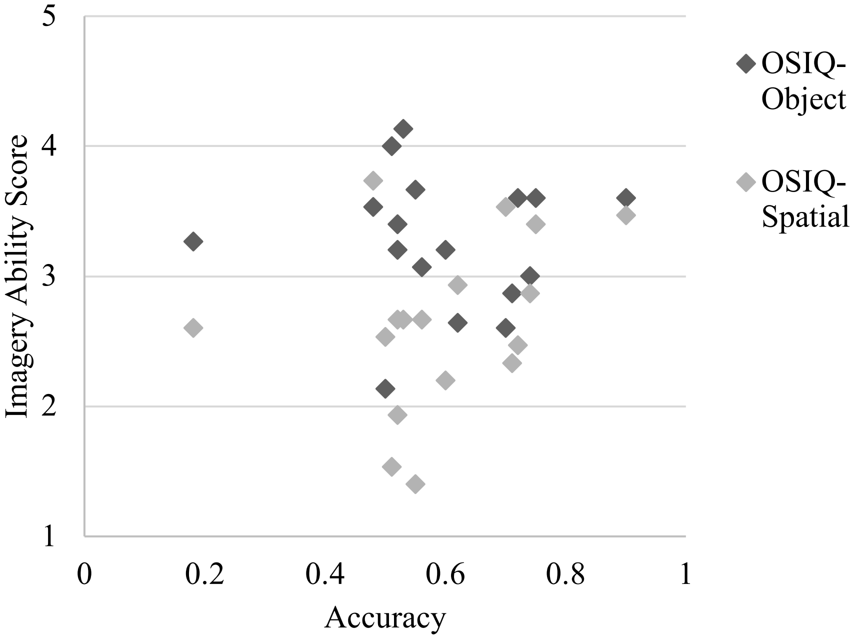

Figure 4.10. Scatterplot of accuracy, measured as a proportion of correct responses, and scores on the OSIQ for object and spatial imagery ability.

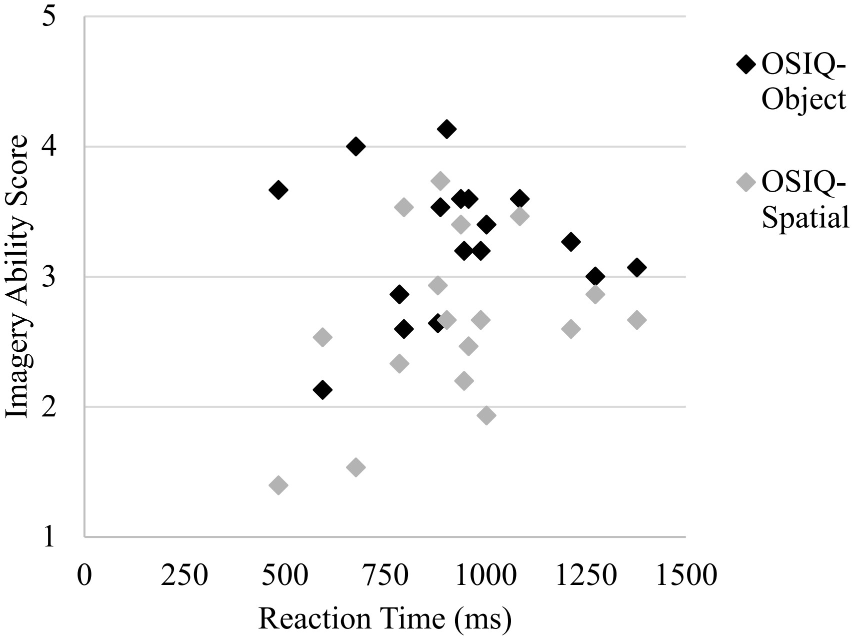

Figure 4.11. Scatterplot showing no correlation between reaction time and imagery ability for either object imagery nor spatial imagery.

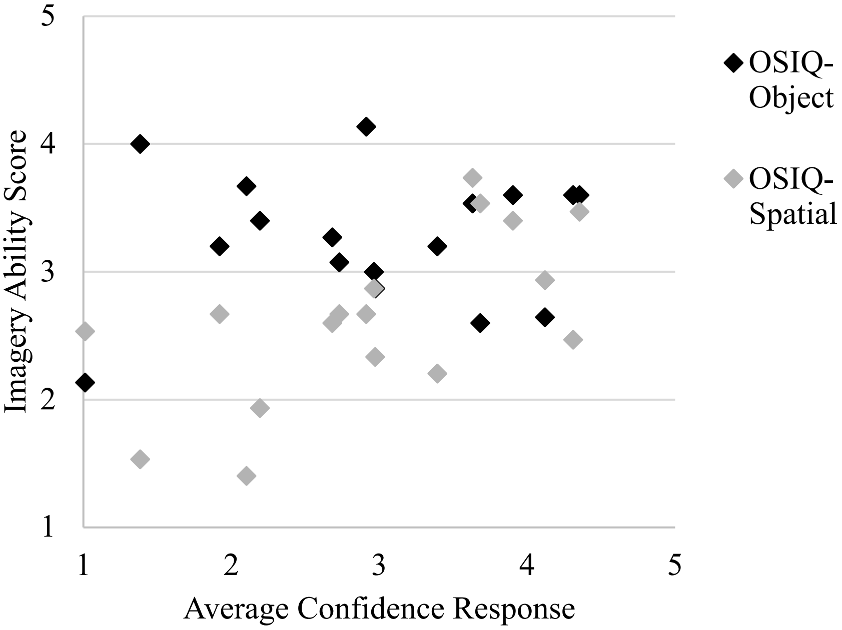

Figure 4.12. Scatterplot of the average confidence response on correct trials and imagery ability scores for object imagery and spatial imagery ability. There is a correlation between OSIQ spatial imagery scores and average confidence for correct responses, but not for OSIQ object imagery scores and average confidence for correct responses.

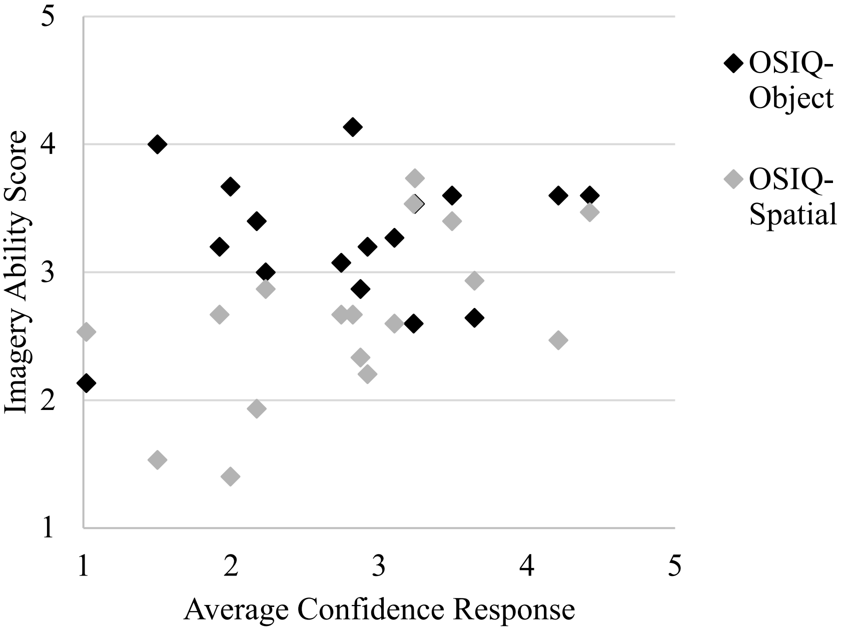

Figure 4.13. Scatterplot of the average confidence response on incorrect trials and imagery ability scores for object imagery and spatial imagery ability. There is a correlation between OSIQ spatial imagery scores and average confidence for incorrect responses, but not for OSIQ object imagery scores and average confidence for incorrect responses.

4.3.3. Experiment 2 Discussion

This experiment investigated associations between self-reported imagery styles of object and spatial imagery, and performance measures of an episodic scene memory task. We looked at the relationship between imagery style and accuracy, reaction time, and confidence ratings. We found no relationship between either imagery style and objective measures of accuracy and reaction time. In regard to confidence measures, the data revealed some moderate correlations that did maintain significance even following Benjamini-Hochberg adjustment. There was an association between spatial imagery score and average confidence rating on correct trials. This association was also present between spatial imagery scores and confidence rating for incorrect responses. These findings suggest that mentally imagery related processes may be relevant for reflective judgments but not objective measures in memory performance.

In relation to objective memory performance measures, accuracy rate did not correlate with either object imagery style or spatial imagery style. Additional, in terms of average reaction time for correct trials there was also no association with either imagery style. The lack of association between either imagery style and both accuracy and reaction time suggest that individual differences in imagery may not be particularly relevant to control for in regard to these objective measures. It suggests no advantage of possessing greater spatial imagery ability for memory performance on scene recognition. However, it must be acknowledge that the small sample size may have resulted in our analysis not able to detect any small effects.

One observation noted during the data collection was the number of comments made by participants during the debrief concerning task difficulty. Despite the task being considered difficult, average accuracy performance was similar across all 3 presentation blocks. This suggests that the learning of the mountain range and the ability to identify the source through rotation was fairly stable over time. A contributing factor to this observation, despite not appearing to disrupt performance, may be the length of time participants were given to make their decision. The length of visual search to both examine the presented scene and make a comparison and transformation to a mental image from memory was potentially quite short.

Whilst this small experiment cannot draw any strong conclusions due to the lack of power, it does provide an interesting foundation for future research to go forward from. I argue that this suggests a proof of principle that individual imagery should be considered carefully in regard to memory tasks. This task required spatial imagery skill and self-reported preference for spatial imagery was related specifically to qualitative judgements about performance. It suggests that when examining subjective aspects of episodic memory, one must also consider individual differences in imagery. From this study, those with a greater preference for spatial imagery are likely to make higher confidence judgements. Applying this to memory research and reflecting on previous studies, higher confidence ratings may be reflective of ease of access to a mental image produced in the mind's eye and individual propensity to manipulate that image rather than a greater 'feeling of remembering'. This experiment further advocates the need for to include individual differences in mental imagery within future research and consider imagery as two separate constructs.

4.4. Chapter Discussion

The aim of this chapter was to explore the relationship between visual mental imagery and memory processes. I examined the contribution of mental imagery as two separate constructs of spatial and object imagery to overcome previous limitations of treating imagery as an undifferentiated construct. To examine if imagery contributed to equally over time, experiment 1 examined the contribute of spatial and object imagery ability to temporally remote and recent autobiographical events. In experiment 2, I examined the relationship between imagery and a lab-based scene recognition task to explore the relationship in an episodic memory recognition task containing both objective and subjective measures. Consistent with previous research, this work demonstrated that imagery does contribute differently depending on task requirements. Object imagery ability was linked to sensory-perceptual details of autobiographical memories both in recent and remote memories. We also found a relationship between spatial imagery ability and scene manipulation confidence. Taken together it highlights that the memory process being examined is very much linked to the type of imagery being used.

One issue with the mixed results of imagery finding in previous research has been due to the memory processes they examine being ill-defined (Aydin, 2018). By using a small portion of the same participants for Experiment 2 that completed Experiment 1, we were also able to examine the link between imagery and a lab-based scene recognition and manipulation task. As expected, Experiment 2 did find spatial imagery ability rather than object imagery ability was related to the task involving scene manipulation. However, the main point of interest was that this was for a reflective process as measured by the subjective rating of confidence; there was no relationship between imagery and objective measures of accuracy or reaction time. On the other hand, object imagery ability predicted several sensory-perceptual details in the autobiographical memory retrieval in Experiment 1. Due to the small sample able to remain for Experiment 2 we cannot draw any strong conclusions, but it does tentatively suggest that even using the same participant sample, imagery contribution varies depending on the memory process being employed by the task.

Across both experiments we found that imagery contributed to reflective judgements. In Experiment 1 these were the ratings of the phenomenological characteristics and in Experiment 2 it was the subjective rating of confidence on decisions related to scene recognition. Whilst evidence does suggest that a pictorial representation of internal information is possible (see Chapter 1), the methodology employed in both experiments does not rule out a propositional argument. The propositional argument would suggest that the experience of a mental image is epiphenomenal; that is, the experience of mental imagery is a result of neural processes in the brain and the experience is a biproduct of that process rather than an actual depiction of internal representation. Therefore, we cannot explicitly confirm that the reflective judgments made are a result of mental imagery occurring. Future work could endeavour to use neuroimaging techniques to explore the neural patterns that support imagery as well as compare results when subjective measures are used.

In conclusion, mental imagery can be divided into spatial and object imagery which contribute differently depending on the memory process being utilised in a task. Although some interesting relationships between mental imagery and memory processes have been demonstrated in this chapter, it does not indicate any causal role of a mental imagery component in memory. Future work is needed to establish if mental imagery is a necessary component across memory processes or utilised when individual ability allows it to be used. Understanding the functional role of imagery in memory has implications for possible therapeutic benefits. Here, I further the work that demonstrates object and spatial ability are separate and measurable constructs that contribute to temporally remote and recent events, as well as reflective processes in recognition memory.

Chapter 5

-

General Discussion

5.1. Thesis Overview

Episodic memory allows the recollection of our personal past as a rich and vivid re-experiencing. It is important for maintaining a sense of self, using past experiences to direct future behaviour (Raby & Clayton, 2012), and providing a shared history with others we can use to facilitate social interactions (Mahr & Csibra, 2018). Examining how memories are recollected subjectively, and understanding the neural substrates underlying the quality of recollection is critical in order to comprehend how events such as ageing and illness can impact on this important process. Therefore, the aim of this thesis was to further understand the processes that support the reliving of a past event in rich, vivid, and multisensory detail. A further focus was whether there were individual differences in mental imagery that contributed to the way we recollect and re-experience a memory. An implicit assumption when asking participants to mentally replay or picture previously observed stimuli is that everyone is able to do so. Yet the presence of mental imagery varies across individuals and not much is known about how this individual difference contributes to episodic memory processes. Through the use of EEG, TMS, and questionnaire methods, the studies in this thesis have provided further insight into how an episodic memory is recollected as a vivid and rich experience, accompanied by sensory reliving. The study in Chapter 2 used EEG to investigate whether the neural oscillations that supported the replay of a prior event differed in power depending on whether the replay was unimodal (only visual or auditory) or multimodal (audio-visual) which required integration of sensory modalities. The experiment in Chapter 3 utilised TMS to determine if the angular gyrus had a causal role in the integration of multimodal recognition and source recollection. The studies within Chapter 4 took a different approach to examining how we re-experience memories. The studies in this chapter considered individual ability to use mental imagery and examined how these differences contribute to memory processes. Specifically, I looked at how difference in mental imagery contributed to both temporally recent and remote autobiographical events, as well as a scene manipulation task to assess how individuals may experience memory differently. I next briefly summarise the results of each chapter. I then discuss the theoretical implications, limitations, future directions and applications.

5.2. Summary of findings

5.2.1. Summary of Chapter 2 results

The aim of the study in Chapter 2 was to examine the oscillatory dynamics that support the replay of rehearsed events that include one modality (either visual or auditory sensory information only) or multiple modalities (both audio and visual information replay simultaneously). Episodic memory is accompanied by rich vivid detail and is not limited to the visual domain; information from multiple sensory modalities comes together to form a unified representation accompanied by a rich reliving experience. Despite event recall usually involving multiple modalities from dynamic situations, much research only looks at each modality in isolation (Quak, London & Talsma, 2015). Neural oscillations are one mechanism that allows communication across brain regions and reflect the collective behaviour of neurons (Buzsáki, 2002). Brain oscillations have been proposed as a vital mechanism for the storage and retrieval of long-term memories (Fell & Axmacher, 2011; Nyhus & Curran, 2010). Oscillations in the gamma frequency band have been linked to context and feature binding (Morgan et al., 2011) whereas in the theta band power has been correlated with recollective states in memory (Guderian & Duzel, 2005; Strunk et al., 2017).

In this study I looked at differences of event-related synchronisation (ERS) and event-related desynchronisation (ERD) of power between modalities and across frequency bands: theta (4 – 8 Hz), alpha (9 – 12 Hz), beta (15 – 30 Hz), and gamma (32 – 68 Hz). Using the same memory replay method as the fMRI study by Bonnici et al. (2016), we hoped to understand the mechanisms that support replay and compare the differences between replay in one modality to replay requiring integration across modalities. We examined the replay period from approximately 1200ms to 4500ms in 9 time windows and at 64 electrode sites.

We expected to find greater power in theta and gamma frequency bands, and reduced power in alpha and beta frequency bands, when comparing multimodal replay to each unimodal replay condition. However, the results of this study did not find any statistically significant difference at any electrode site in any of the time windows or electrode sites for all four frequency bands of interest. Decreases in power within alpha and beta frequency bands have been linked to the representation of stored information (see Hanslmayr et al., 2016). Therefore, it is surprising we did not find any windows or electrode sites of difference between modalities here. It cannot be completely ruled out that no difference existence between modalities. One possibility is that because we examined power changes over a long time period, previous indications of ERS/ERD may occur earlier during a temporal event and are not maintained during replay. Additionally, the exploratory parameters of analysis meant that there was a wide window of interest, therefore it is possible that a more focused grouping of electrodes of interest would reveal significant locations of interest. Gamma power has been connected with a rich memory state of recollecting rather than familiarity (Burgess & Ali, 2002). Therefore, it is possible we found no significant differences in power for gamma between the unimodal and multimodal conditions because they were all equally being recollected. Additionally, theta has been suggested to be a domain general process (Hanslmayr, Staudigl, Aslan & Baunl, 2010; Staudigl, Hanslmayr & Bauml, 2010). Our findings support this supposition and extend it to also being general across modality of replay.

The examination of imagery ability with both the vividness and consistency ratings collected during replay yielded intriguing results. As a measure of visual imagery, the VVIQ purports to measure self-reported vividness for visual imagery. Yet here we found no association with VVIQ scores and the vividness of any modality of replay. It may suggest that vividness ability has no bearing on how likely one may vividly experience a replayed memory in each modality. In constrast, the BAIS-V, a measure of vividness in auditory imagery, was associated with higher vividness ratings in auditory as well as visual modalities. Despite a measure designed for auditory imagery, it suggests that vividness of imagery for visual and auditory modalities may be hard to unpick. Interestingly, there was no association with the vividness rating for multimodal replay despite being an integration of both auditory and visual components.

Two possible explanations of these findings may explain this paradox. Firstly, the measures of mental imagery used in this experiment may be too broad. For example, mental imagery may not be unitary construct (Kosslyn et al., 2001; Thompson et al., 2009), with some work suggesting it can be divided into spatial and object imagery (Blajenkova et al., 2006). The VVIQ treats imagery as one construct and therefore may have not detected any association with vividness experienced in each modalities because it was too general in the imagery ability it was assessing. Similarly, the BAIS may not be valid to make connections beyond the auditory domain for which it was designed. A second explanation is that individual imagery ability relates to modality differently when it requires integration during recollection. Further work is necessary to both examine the presence of individual differences in mentla imagery and its relationship to experiencing memory as a vibrant multimodal reliving.

5.2.2. Summary of Chapter 3 results

The aim of the study in Chapter 3 was to explore the behavioural consequence of disrupting processes supporting episodic memory for item with unimodal and multimodal features. Previous work has associated the left angular gyrus as a convergence site for the binding of sensory information together into a unified representation (Damasio, 1989; Shimamura, 2011). Its position at the junction between several cortical regions puts it at an optimal position to receive and integrate information from across the cortex (Seghier, 2013). It has been suggested that it is the binding of the sensory information into a complete representation within the angular gyrus that allows and enhances a vivid event memory (Moscovitch et al., 2016; Ramanan et al., 2018; Rugg & King, 2017; Simons et al., 2010). Examining the behavioural consequences of disrupting the left angular gyrus using TMS was important for two reasons. Firstly, unlikely imaging methods, TMS provides an avenue to establish causality. By disrupting a cortical site and examining the behavioural consequences compared to a control area it can be establish if a site is indeed necessary for the behaviour. Secondly, TMS can allow the creation of a temporary virtual lesion, unlike patient studies, the consequences of disruption in a test condition can be compared to a control condition in a within-subjects design.

In this study, we targeted stimulation at the left angular gyrus and compared the behavioural responses of item recognition, source recollection, and confidence for items highly associated with either unimodal or multimodal features against the responses at a control site of the vertex. If the left angular gyrus is necessary to bind together the multimodal features of an item at recognition which impact the subjective experience, then we expected to find a difference between the stimulation and control sites for the multimodal condition particularly for the confidence judgments about the source. Recollection of the source would require contextual reinstatement, and the confidence judgement based on this would therefore be reduced when the angular gyrus functioning was disrupted. We did not expect that recognition judgements would vary as this would not specifically require a representation of the item learnt at encoding. Nor did we expect unimodal conditions of visual/auditory would be impacted due to the stimulation if the angular gyrus is not necessary for unimodal information binding.

This study found a trend of a reduction in source recollection confidence for multimodal items following angular gyrus stimulation compared to control. While this did not reach statistical significance, it is likely that by increasing the sample size and thereby power of the study, this could achieve significance. Finding no difference in recognition accuracy and recognition confidence, nor source recollection accuracy, was not unexpected and in line with previous studies that suggest the angular gyrus is not required for performing recognition memory decisions (e.g., Ciarimelli et al., 2017; Yazar et al., 2014; 2017). Similarly, for the unimodal conditions we did not find any differences between angular gyrus and control stimulation. One finding that we did not anticipate was a main effect of modality. The confidence for auditory items was significantly lower than that of both visual and multimodal items in both stimulation conditions, suggesting the auditory memory is not equivalent to either visual or multimodal memory modalities at recollection. Overall, from this work we cannot completely support that the angular gyrus does underpin the feature integration of multimodal items that in turn enable a vivid recollection. While we did see a trend in reduced confidence for source recollection judgements of multimodal items following angular gyrus stimulation suggestive of some effect, the parameters of this study cannot support this to a statistically significant degree.

5.2.3. Summary of Chapter 4 results

The aim of chapter 4 was to examine the contribution of visual mental imagery to episodic memory processes. Previous research has linked visual mental imagery to experience a sense of reliving in memory (e.g. Greenberg & Knowlton, 2014; Irish, Lawlor, O'Mara & Coen, 2011; Rubin, Schrauf & Greenberg, 2003). In extreme cases where individuals report no use of mental imagery, a condition termed aphantasia, they also report less vivid and rich autobiographical memories (Dawes et al., 2020). The vividness of visual imagery ability has also been correlated with the strength of event recollection (Rubin, 2005), visual details, and representation of spatial information (D'Argembeau & Van der Linden, 2006). However, other work has found that vividness of visual imagery is not correlated with reliving or the presence of visual images (Greenberg & Knowlton, 2014). It suggests that vividness may not be the best measure to assess mental imagery.

The mixed findings on what the precise contribution of imagery to memory has been attributed to treating imagery as a unitary construct and generalising across memory processing (Aydin, 2018; Sheldon et al., 2016; Vannuci et al., 2016). Object imagery refers to the representation/appearance of objects such as colour, size, and shape. On the other hand, spatial imagery refers to the representation of spatial relations between objects, or parts of objects, to each other and spatial transformations. Higher object imagery has been linked to faster retrieval times of autobiographical memories and a greater number of sensory-perceptual details (Vannuci et al., 2016). Spatial imagery seems to be relevant for binding elements of a scene and disrupting encoding in individuals with higher spatial imagery has a greater detrimental effect on recognition (Sheldon et al., 2016). In sum, object imagery has been suggested to relate to reflective processes, whereas spatial imagery is more related to retrieval processes (Aydin, 2018). Although to my knowledge this had not been investigated in regard to the age of memory or where scene manipulation was required for accurate recognition.

In Chapter 4, I focused on spatial imagery and object imagery as two separate constructs of imagery, using an established self-report measure to gauge individual ability of both spatial and object mental imagery (OSIQ; Blajenkova et al., 2006). In Experiment 1, I examined the contribution of both spatial and object imagery ability to autobiographical memory that vary in temporal distance: remote memories that occurred over 10 years ago, and recent memories that had occurred within the past 2 weeks. The results demonstrated that object imagery ability, but not spatial imagery ability, was related to several phenomenological characteristics of autobiographical memory recollection. For recent memories, object imagery ability predicted the experience of reliving, the presence of feelings associated with the original event, the presence of visual details, generation of imagery, and the layout of the event. For remote memories, object imagery ability predicted the experience of reliving, the presence of feelings associated with the original event, the presence of visual detail, generation of imagery of the event, experiencing mental time travel, belief the event occurred as it was originally, and rehearsal.

The results here show object imagery ability predicted slightly different phenomenological characteristics for recent and remote memories. It implies that the benefit of object imagery ability changes depending on how old the event memory is and may also suggest a change in the way recent and remote memories are represented. Research suggests a link between the ventromedial prefrontal cortex (vmPFC) and the hippocampus, with vmPFC guiding context-relevant mental imagery representations in the hippocampus (Barry et al., 2019). Additionally, Bonnici et al. (2012) have shown that remote memory patterns are more detectable in the vmPFC and hippocampus compared to recent memories. Taken together with our findings, it suggests that the construction of an internal representation may differ depending on the age of a memory and that the ability to use imagery may predict how successful the construction is particularly for remote memories. Further investigation would be needed to confirm this by examining the neural patterns of memory recollection while taking into consideration imagery ability.

In Experiment 2 of Chapter 4, I turned to a memory recognition task to explore the link between imagery and memory for a lab-based tasks involving scenes. Participants learnt to recognise two scenes and were then asked to recognise these scenes presented at different angles. Here, I found that neither object or spatial imagery ability was correlated with accuracy or reaction time. There was a significant positive correlation between spatial imagery ability and confidence judgements. This was the case for both correct and incorrect responses. It may demonstrate a tendency of those with higher spatial imagery ability to be have greater confidence in reflective decisions, regardless of whether they are accurate or not.

An additional aim within Chapter 4 was to assess the relationship between different imagery measures. Although the VVIQ (Vividness of Visual Imagery Questionnaire; Marks, 1973) is a commonly used measure of imagery ability, it does not differentiate between imagery types. The VOSI (Vividness of Object and Spatial Imagery Questionnaire; Blazhenkova, 2016) on the other hand does measure vividness of object and spatial imagery separately. We compared the self-reported scores of these two vividness of imagery questionnaires to the OSIQ. Our results were in line with other work that the OSIQ measures two unrelated imagery constructs (e.g. Aydin, 2018). We found the OSIQ spatial imagery scores correlated with the VOSI spatial scores. The OSIQ object imagery scores correlated both with VOSI object as well as VOSI spatial scores, suggesting the questionnaires do not map directly the contribution of vividness of each construct. The VVIQ scores correlated with the OSIQ object scores, but not OSIQ spatial scores, unlike other work (see Aydin, 2018).

The results of this work suggest that object imagery ability does contribute to reflective processes of recollection as indicated by phenomenological characteristics of autobiographical memory recollection. Critically, object imagery ability predicts a sense of reliving and visual details for both temporally recent and remote memories. However, object imagery ability predicted more characteristics for temporally distance events including experiencing a sense of mental time travel. Interestingly, this work found that spatial imagery ability is also related to reflective judgements of confidence when reflecting on the spatial layout of a scene but had no relationship to objective measures of retrieval. In conclusion, I suggest that this work demonstrates imagery contributions do differ depending on whether we examine object or spatial imagery. Furthermore, the memory process that is being assessed can be linked differently to imagery. Both object and spatial imagery ability have been linked to reflective processes, therefore I suggest that it is the content of the task being conducted that links to memory.

5.3. Theoretical implications

5.3.1 Sensory modality in creating a contextual representative which enables a rich subjective re-experience of episodic memory.

The integration of sensory modalities is a topic of interest in episodic memory, as is the exploration of how we are able to richly relive past events. The two factors are interlinked: episodic memory is usually accompanied by a vivid sense of reliving sensory information, such as what was seen and heard. The sensory information needs to be integrated to enable a unified representation. The parietal cortex has attracted a great deal of attention in regard to its possible role in episodic memory. Neuroimaging demonstrates parietal activation in successful retrieval of episodic memory (Rugg & Vilberg, 2013; Wagner et al., 2005; also see Rugg & King, 2018). However, patients with parietal lesions still display intact recognition memory although their sense of reliving appears to be impaired (Berryhill et al., 2007; Simons et al., 2010). Additionally, these patients report less sensory-perceptual details during recall (Berryhill et al., 2007; also see Irish et al., 2015). It highlights a link between the qualitative side of episodic memory and multimodal integration. Therefore, in Chapter 2 and 3 we explored the differences in unimodal and multimodal episodic memory.

The work in Chapter 2 did not find any power related differences in neural oscillations across auditory, visual, or multimodal (audio and visual simultaneously) replay of remembering video clips. It would suggest that the memory replay over sensory modalities, even when requiring integration, uses similar neural oscillatory dynamics to support the experience. Theta power has been linked to successful recollection (e.g. Guderian & Duzel, 2005; Strunk et al., 2017). Finding no difference particularly in the theta frequency band would support the notion that theta is a general mechanism not sensitive to material type (Khader & Rosler, 2011). Here, we extend this to being general across sensory modality too to support successful recollection. Similarly, power within the gamma frequency band has been connected with recollection rather than familiarity (Burgess & Ali, 2002). We suggest that the absence of any gamma power differences between modalities would indicate both the unimodal and multimodal conditions can result in an equal recollection experience. Interestingly, this work did not find any localised power difference even in parietal electrode sites. This is particular surprising considering the links between parietal sites and modal integration (e.g., Bonnici et al., 2016). We consider that the design of our experiment may not have been specific enough to detect any differences in the topography of the conditions.

The study in Chapter 3 focused on the left angular gyrus within the parietal cortex in particular. This region has been proposed as a suitable site for the binding of sensory information (see Rugg & King, 2017; Seghier, 2013). Accounts that propose the role of the left angular gyrus include the subjective integration hypothesis that the binding of sensory information allow the subjective re-experiencing (Moscovitch et al., 2016; Simons et al., 2010). Similarly, the Contextual Integration Model proposes the binding and representation of multimodal contextual information (both sensory and emotional details) that enhances the experience of vivid event construction (Ramanan et al., 2017). The multimodal hypothesis argues it is the integration of multimodal features that underpin the subjective recollection moreso than single modality (Bonnici et al., 2016). In line with what would be expected from these accounts, this work did not find differences in recognition accuracy when the angular gyrus was disrupted with TMS for either unimodal or multimodal conditions. It supports that this region is not strictly necessary for recognition memory judgements. In contrast to what would be predicted from these accounts, we did not find a significant reduction in confidence of source memory judgements from disruption of the angular gyrus for multimodal items. Despite the findings suggesting a trend in the expected direction, we are unable to draw any strong conclusions regarding the role of the angular gyrus in multimodal integration on subjective source judgements.

It does raise a question as to whether the role of the angular gyrus is solely to integrate multimodal, perceptual details that in turn allow vivd reliving of episodic memories. The angular gyrus may provide a platform to bind perceptual features together and if recollection is required it may draw upon this representation. Is possible that the very nature of a multimodal memory is richer in vivid re-experiencing, engaging the angular gyrus to a greater degree to support the binding. That is to say it is not possible to have a vivid re-experiencing of a single modality in memory, but that angular gyrus contributes to support the integration and coordination across the cortex to enable vivid reliving of more complex situations.

Across the three experimental chapters our results highlighted that modalities are not remembered equally. The studies within Chapters 2 and 3 found that memory judgements for vividness and confidence about auditory stimuli were lower than both multimodal and visual stimuli. Similar, in Chapter 4 the average number of auditory details recalled in autobiographical memories was less than that of visual details. Other work has demonstrated that auditory stimuli is inferior to other modalities (e.g., Bigelow & Poremba, 2014; Cohen et al., 2009). Here we too demonstrate that auditory memory is poorer than that of visual and multimodal memory across replay vividness, recognition confidence, and event characteristics. It suggests that comparing multimodal memory to auditory memory alone may not be a practical comparison to discern meaningful results. Arguably, we always have a visual sensory input, with the notable exception of those who are visually impaired, that accompanies auditory input. Even within the studies of Chapters 2 and 3 the auditory encoding was accompanied by a fixation cross during the sounds. Although silence too could arguably be an input itself (a question for another thesis to explore), the findings of this thesis suggest that auditory stimuli is simply unequal to that of another unimodal modality of visual stimuli and that of multimodal stimuli of auditory and visual sensory modalities together.

5.3.2. The contribution of visual imagery in subjective re-experiencing of episodic memory.

Whilst neither Chapter 2 nor 3 aimed to measure the specific role of imagery in recollection, Chapter 4 aimed to directly assess the contribute of mental imagery on the experience of memory. Specifically, it aimed to explore individual differences in spatial and object imagery abilities. Despite indications that imagery can be experienced differently (e.g., Galton's breakfast table scenario; see Chapter 1), it has only been more recently that these differences in mental imagery have attracted interest (see Zeman et al., 2015). Because of this, there appears to be a greater acknowledge of the possible impact the variation could have, but much work is still needed in this area.

A key point that has been demonstrated in this work is that there are individual differences in the contribution of mental imagery to memory process that depend on imagery ability (see Chapter 4). This has implications about the language and measures we use and when asking participants to provide ratings in memory studies. For example, the study in Chapter 2 asked participants to indicate how vividly there were able to replay a learnt video clip. Yet an assumption here was that all participants experienced an internal mental representation and were able to comment on how vivid that experience was equally across modalities. Research on aphantasia (a condition characterised by a lack of mental imagery) suggests it is expressly a lack of sensory and phenomenal imagery, rather than a lack of metacognition or awareness of there being an internal mental image that exists (Keogh & Pearson, 2017). Regarding the language we use around instructing participants to “picture in the mind’s eye” there needs to be a general awareness that not everyone has the ability to do this and this ability could be a scale. Therefore, this is something that needs to be considered, especially if the experimental task implicitly requires the generation of an internal replay as it did in Chapter 2.

A further important contribution our findings make is that it supports other work showing that spatial and object imagery are two unique constructs, rather than mental imagery being a unitary construct. Previous work has demonstrated that object imagery ability contributes to reflective processes in the recollection of autobiographical past whereas spatial imagery ability contributes to event detail retrieval for both autobiographical thinking of past and imagined future events (Aydin, 2018). Here we expand this by demonstrating that object imagery contributes across temporally remote and recent memories for the phenomenal characteristics of autobiographical memory. However, for an episodic memory task of recognition and scene manipulation, we did not find any relationship between measures of accuracy or ease of retrieval with spatial imagery. We did find a relationship between spatial imagery and confidence of responses, suggesting in this process reflective judgements too relate to spatial imagery. It overall suggests that the contribution of imagery to more memory processes needs be characterised to precisely understand the processes imagery relates to.

While the work of this thesis has examined modality integration and visual mental imagery for enabling a rich recollection of past events, it is possible that the two elements actually overlap. Ramanan et al. (2018) suggests that scene construction is underpinned by both visual imagery and contextual integration processes. Their work examined Posterior Cortical Atrophy (PCA), a rare neurodegenerative condition characterised by a reduction as visuospatial and visuoperceptual skills (Crutch et al., 2012). They found a distributed set of posterior parietal regions modulated the overall richness in scene construction; they propose that it is the combination of a deficit in visual imagery and integration processes that explain why PCA patients have a scene construction deficit. The neural correlates of visual imagery have been linked to the left superior parietal lobule (Winlove et al., 2018) and the left angular gyrus within the posterior parietal cortex for building an integrated representation (see Rugg & King, 2017; Seghier, 2013). It is therefore possible that links between both regions and to the hippocampus work to build a scene representation in complete a memory process (see Scene Construction Theory;

Hassabis et al., 2007; Hassabis & Maguire, 2009; Maguire & Mullally, 2013; Maguire et al., 2016; Mullally et al., 2012). The combination of visual imagery and contextual integration could also explain why mixed results exist when only one aspect has been considered. Additionally, if a task can be accomplished without the need for scene construction (e.g., recognition memory) then it can explain why we see no difference in memory performance measures. This thesis examines modality and mental imagery, but the implications from our findings may need to be considered in tandem to fully understand how a rich recollective experience is enabled for episodic memory.

Of further interest in regard to imagery is the viewpoint from which a memory is recollected. There are two types of frames which an individual can represent spatial information: allocentric and egocentric. An allocentric frame considers the relationship of objects to each other within space, creating an 'observer' perspective. On the other hand, an egocentric frame focuses on the subject to object relation and leads to a self-centred perspective as if from one's one eyes (for a review see Colombo et al., 2017). In general, recent autobiographical memories are associated with an egocentric perspective while remote autobiographical memories take an observer perspective (e.g., Nigro & Neisser, 1983; Rice & Rubin, 2009). Switching between perspectives of allocentric and egocentric representations is necessary for imagery in memory retrieval and mediated by posterior parietal regions (Byrne, Becker & Burgess, 2007). It would suggest that the perspective taken in recent and remote memory recollection could use object and spatial imagery abilities differently. Individual differences in imagery ability could therefore also impact the use of this perspective shifting and thereby change the experience of the recollection. Egocentric strategies are supported by an extended area of activiation involving the right superior occipital gyrus, angular gyrus and precuneus (Boccia et al., 2014). Posterior parietal cortex shows activity during shifting of visual perspective during memory retrieval (St Jacques, Szpunar & Schacter, 2017). Additionally, the left angular gyrus has been suggested to supports the building of multimodal features into an egocentric framework (Bonnici et al., 2018). Taken together with the role of imagery, it could be that the angular gyrus and mental imagery provide complementary roles in the establishment of a vivid recollective experience.

5.4. Limitations

It is necessary to address several limitations present in the experiments of this thesis. One methodological limitation in the study in Chapter 2 was the window of replay that could be examined using time-frequency analysis. The six second replay clip was initiated by a cue word and the end of replay was signalled by an auditory tone. Therefore, either end of the segment for analysis did not contain uncontaminated data to be used as a baseline: the start would likely have neural processes related to retrieval, rather than replay; and the end would include any neural response from hearing the tone. Baseline correction was completed by averaging the activity over all trials to create the baseline and then that was subtracted from each modality. A better method may have been to ask participants to indicate when they had completed the mental replay: it would have removed the auditory contamination for the end of the segment and would have provided an indicate that participants had managed to temporally replay the clip similar to encoding. Alternatively, a baseline recording of neural activity that was not task related such as asking participants to close their eyes and sit quietly would have provided a comparison recording. Whilst this has its own limitations, such as not know if the participants were engaging in rehearsal, it would be an interesting comparison to compare mind wandering activity to that of event replay.

A substantial limitation of the study presented in Chapter 3 is the presence of ceiling effects. Despite efforts to avoid this by checking the data of the first two participants collected, it is possible that the task difficulty was simply not great enough and lead to participants reaching maximum scores. However, this was potentially unavoidable. A methodological limitation of TMS itself is the time frame that any effects of neuronal disruption can last. Offline stimulation can have after-effects of up to an hour, returning to baseline activity after 60 minutes (Bergmann et al., 2016). Research suggests that a window of 25 to 45 minutes may be optimal to still observed effects (Huang et al., 2005). Therefore, the design of our study had to factor in this temporal aspect during the completion of the test phase. Our test phase lasted a maximum of 30 minutes to ensure we fell into this window. If we had increased the number of trials to also increase task difficulty, we would have encountered difficulties in ensuring the temporal effects of the TMS stimulation were still present.

Although the presence of ceiling effects does put some limit on what can be interpreted from the study, the subjective measures do still provide insight into the experience of memory recognition and source recollection. While the high accuracy of recognition means we are unable to detect differences in the higher end of the scale, the confidence responses provide a subjective index of the experience of the recollection. One alternative to our employed design would be to test each modality in separate blocks, moving from two testing session (one for each stimulation site) to six testing sessions (two sessions for each modality, one for each stimulation site). This would provide a greater scale for the accuracy as well as more responses to examine the subjective measures. However, this too has consequences such as the greater expense and the higher possibility participants may withdraw or miss sessions.

An additional limitation of the study in Chapter 3 is that the sample size is admittedly small when considering the method of localisation for the TMS stimulation. It is possible that we may not have accurately targeted the angular gyrus for each individual. This may be a factor in why our study did not reach statistical significance in the findings. There are several methods that can be used to decide localisation, with some being more tailored to individual anatomy and based on functional activity than others. The more specific a method is to an individual both from a structural and functional perspective, the lower the sample size required to observed similar effects (Sack et al., 2009). The method we employed for localisation was to use a standard anatomical scan (MNI 152) and morph it to markers on each individual. The co-ordinates we used to locate the angular gyrus were taken from other TMS work looking at the angular gyrus which did find significant differences after stimulation at the site using a similar continuous theta burst protocol (e.g., Bonnici et al., 2018; Yazar et al., 2014; 2017). There seems to be a large amount of inter-individual variability between boundaries of areas within the ventral lateral parietal cortex (Caspers et al., 2006). Therefore, it is more likely the localisation via morphing the average scan to different head shapes is the concern rather than the site co-ordinates for stimulation or the protocol. A more individualised approached, for example using the anatomical scans of each individual, would have ensured we were always targeting the angular gyrus. Due to the resources we had available, we were unable to acquire MRI scans for each individual therefore we used a more affordable alternative. The localisation method we employed here does present a cheaper alternative to individualised localisation methods, but it does come with a need for a greater sample to detect differences and a greater chance of error that must be considered when interpreting any findings.

A limitation to consider in Chapter 4 is the method of interview collection. A typical method of assessing autographical memory is to conduct an interview and subsequently transcribing the detailed memory descriptions participants generate (e.g. Levine et al., 2002; St Jacques & Levine, 2007). Experiment 1 of Chapter 4 asked participants to write a detailed description of an event rather than being conducted as an interview that was recorded and then transcribed afterwards. It is possible the in-person interview is richer and more detailed compared to being asked to write about an event. The experience may feel more informal and like a conversation promoting a freer recall of the event rather than having to produced structured sentences in a written format. Additionally, the level of writing ability may differ across participants where the wording participants may use in speech varies to what they produce as written text. The spoken interview also provides the opportunity for prompt when participants may struggle with elaborating, something which an online experience cannot provide. Asking participants to write a detailed description has been used in other work (e.g. Aydin, 2018) therefore it a viable and comparable method of collecting data about event memory. The best way to determine if this is a limitation would be to compare the responses within the same individuals when data is collected via both methods. As it stands, collecting responses via written description is a perhaps more accessible method to reach more people that may not be able to attend an in-person interview.

A limitation we must acknowledge across the studies within both Chapter 2 and 3 is that we treated all modalities as equal in memory. Visual memory is generally very accurate even for a large number of stimuli (e.g., Standing, 1973; Brady et al., 2008). In comparison, auditory performance is generally worse at longer retention times (Bigelow & Poremba, 2014) and does not match performance for that of visual stimuli (Cohen et al., 2009). The study in Chapter 2 had a considerably long time between the encoding and retrieval of the video clips. It is likely that the retention of the audio clips, despite being rich/vivid at encoding, may have not been as reliably retained at replay compared to the multimodal and visual clips due to this time period. Similarly, the study in Chapter 3 examined memory for items that had high modality features (e.g. a siren would be more associated with auditory features, a book more associated with visual features). It is then questionably as to whether the comparison between modalities is fair; it is possible that differences in performance across modalities is due to non-equivalence of stimuli (Visscher et al., 2007). It is also somewhat unlikely to have memory of auditory without any sort of visual accompaniment. The exception is of course individuals with visual impairments but generally in the experience of everyday events, we receive a great deal of sensory input and often not auditory in isolation. However, a counterpoint to this is adjusting for the non-equivalence is not representative of a real-world memory. The aim of this work was not to assess the equivalence of modalities, but rather the experience of remembering across modalities. Whilst I suggest this needs to be taken into consideration, the nature of memory in a real-world scenario is often not completely equivalent and as such our comparisons have worth by not manipulating the auditory equivalence by degrading visual stimuli.

Finally, a general limitation across all of the studies in this work is the subjective nature of what is being investigated. While the central aim of this thesis is to explore the mechanisms and contributions that allow the experience of episodic memory as a rich and vivid re-experiencing of past events, it is heavily reliant on measures of self-report and introspection of the experience during the memory processes. Whilst this in itself is not a problem as we are interested in the experience and how participants experience memory replay, recognition, and recollection, it cannot be ignored that there are limitations in exploring such a subjective topic.

In Chapter 2 we did not have any objective measure of whether the replay was successful for all modalities and were heavily reliant on participants fully engaging in the task honestly. Therefore, even if the mechanisms of memory replay were similar across modalities, the experience of memory replay may not have been equivalent across participants and is still subject to individual capability and interpretation. An additional consideration is how we indexed subjective experience. In Chapter 2 we assessed vividness for the memory replay, and for Chapter 3 we collected confidence in the judgments made. For Chapter 4, Experiment 1 examined the ratings given for phenomenological characteristics of event memories and Experiment 2 also used confidence responses. This wide range of subjective measures may not be enough to determine the full picture of what is occurring in regard to the phenomenon of re-experiencing. Key features of episodic memory are the rich recollection of the sensory-perceptual details which are re-experienced as if the event itself was occurring again and involving a subjective sense of time. Our approach tries to quantify the subjective experience of reliving and assumes that this is possible through the use of subjective ratings on confidence and vividness. Whilst this is not wrong, it must be considered in how we interpret the findings. For example, it is possible that one can be highly confident and ‘remember’ the event, while both being wrong or not having an internal scale than defines confidence in an equal manner across all memories.

5.5. Future directions and applications

Memory of previous events is essential for learning, for developing a sense of self, and being able to draw on experiences to imagine future events built from past knowledge. Understanding the underlying mechanisms that support cognitive processing of episodic memory is vital for developing effective interventions that help overcome deficits in memory performance both in healthy ageing and clinical populations. Exploring the neural patterns that underpin replay of episodic memories and determining the behavioural consequences when we disrupt networks considered responsible is one step towards building the bigger picture in understanding episodic memory. Further, knowledge about how individuals re-experience and whether this is similar across the population is of great importance is determining what variations should be consider when investigating memory and possible interventions.

One factor we have not considered in this thesis but would present an interesting area for future work is the congruency of modality. In this thesis we look at multimodal integration and how that supports the subject experience of memory, but we constrained the multimodal features to those that are related (e.g., the sound of running water with a picture of a water fountain). However, multimodal information can also be unrelated (e.g., the sound of running water with an egg cup). It would be interesting to investigate if the contextual representation that is hypothesised to enable a rich recollection experience is specific to related features or if it is general integration of information that is unimpacted by congruency. Additionally, we only looked at the integration of congruent audiovisual stimuli. Therefore, another interesting avenue would be to explore the integration of other modalities, such as visual with olfactory memory.

Our findings have demonstrated a contribution of mental imagery, particularly object imagery ability, in the recollection of past events. Additionally, our findings suggest that theta power may be a domain general mechanism that does not discriminate across modality. Other work has indicated the importance of theta phase in vivid visual imagery of autobiographical memory (Fuentemilla et al., 2014) and indicated that beta frequency is involved in the cross-modal integration of visual and auditory imagery (Villena-González et al., 2018). Furthering our work to examine oscillations of memory replay and comparing to neural oscillations of mental imagery may provide some insight into whether there is overlap between the mechanisms that support these processes both involved in memory.

The advancements in research techniques keep allowing greater leaps in knowledge as we apply them to interesting questions in the pursuit of understanding human memory. TMS is a fascinating methodology which is growing in application as we further understand the impact of a variety of different protocols. For example, instead of disrupting the angular gyrus using an inhibitory protocol, if an excitatory protocal could be applied it would be interesting to see if there were memory benefits present such as increased integration and greater recollection. Transcranial direct current stimulation (tDCS) is another non-invasive stimulation technique used to modulate cortical excitability using anodal and cathodal currents. A positive anodal current is expected to result in facilitated behvaiours and a negative cathodal current inhibits behaviours (Nitsche et al., 2008). By having a direct comparision of both facilitory and inhibitory stimulation within a participant we could examine memory performance and experience after targeting the posterior parietal cortex to further investigate its role in qualitative aspects of episodic memory.

A further particularly promising avenue is the combination of TMS and EEG methods (see Miniussi & Thut, 2010). With the right lab set up with space for EEG equipment and TMS equipment located close together the techniques can be combined. As long as the TMS stimulation does not co-occur with the period of interest recorded by the EEG, the advantages of determining causality provided by TMS can be used in conjunction with recording the neural activity that occurs when you interpret the typical neuronal firing. For example, a late positive component typically found at left parietal sites in EEG studies is associated with episodic recollection rather than familiarity (e.g., Ally et al., 2007; Turk et al., 2018) and has been linked to memory judgements (Yang et al., 2019). TMS could be used to determine the consequences to a wider neural network when disrupting a region thought to be interconnected, such as the angular gyrus with its connections to other sensory cortices. Additionally, the parameters of TMS could also be manipulated to see if functioning could also be enhanced to see if we could improve recollection via stimulation of parietal sites.

There is a growing body of research exploring neural oscillations that support a variety processes, but much is still possible to explore due the wide range of parameters that can be implement in both design and analysis. A further advantage of utilising EEG to examine neural oscillations is that it offers a method of assessing how brain regions may communicate during memory processes in a more affordable way compared to fMRI. Additionally, it is especially useful in situations where a participant may not be able to use other imaging methods such as fMRI, such as older adults and individuals with dementia. By understanding the mechanisms in a neurotypical population we can go on to establish differences seen in neurodegenerative illness where there is a decline in memory, such as dementia. Furthermore, it could also help determine if there is age related differences in the recollective experience of episodic memory.

We have demonstrated that mental imagery contributes to the experience of certain characteristics of autobiographical memory, including reliving. If we know that aspects of mental imagery contribute to the experience of autographical events, even temporally remote events, we can consider how this can be used to an advantage, especially in age related memory disorders and just general decline in cognitive abilities in healthy ageing. It would be beneficial to determine if object and spatial mental imagery ability is stable across age. Firstly, it would help determine if there is an advantage of possessing imagery abilities in older age as a way to protect memory of our past. Secondly, it would indicate if imagery contributed to reliving across the lifespan. If it was the case that imagery ability provided some benefit in protecting memory in ageing, it would also be interesting to determine if this ability could be improved through mental training.

5.6. General conclusion

In conclusion, the research presented in this thesis has demonstrated that modalities and mental imagery both play an important role in the subjective re-experiencing of episodic memories. First, we suggest that neural oscillations supporting the replay of episodic events are similar across sensory modalities. Secondly, while we did not reliably find evidence for the role of the angular gyrus in multimodal integration that supports rich reliving, we do suggest this work provides insight into a possible reduction in confidence for multimodal source recollection when typical neuronal function is interrupted. Finally, we have also provided further evidence that visual mental imagery can be considered as two separate constructs of object and spatial imagery, which each contribute to separate aspects of episodic memory processes. We have demonstrated that object imagery predicts phenomenological characteristics both for temporally remote and recent event memories. This thesis has contributed by furthering our understanding of how episodic memories are recollected as a multimodal, rich, and vivid re-experiencing. It has explored the experience of episodic memory through looking at the replay, recognition, and recollection of memory, with a focus on sensory modalities and mental imagery determining this are key elements to consider in episodic memory reliving.

References

Addante, R. J., Watrous, A. J., Yonelinas, A. P., Ekstrom, A. D., & Ranganath, C. (2011). Prestimulus theta activity predicts correct source memory retrieval. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(26), 10702–10707. https://doi.org/10.1073/pnas.1014528108

Ally, B. A., & Budson, M. D. (2007). The worth of pictures: Using high density event-related potentials to understand the memorial power of pictures and the dynamics of recognition memory. *Neuroimage*, *35*(1), 378–395.

Atkinson, R.C. and Shiffrin, R.M. (1968) Human memory: a proposed system and its control processes. In The Psychology of Learning and Motivation: Advances in Research and Theory (Spence, K.W., ed.), pp. 89–195, Academic Press

Atance, C. M., & O'Neill, D. K. (2001). Episodic future thinking. *Trends in cognitive sciences*, *5*(12), 533-539.

Aydin, C. (2018). The differential contributions of visual imagery constructs on autobiographical thinking. *Memory*, *26*(2), 189–200. https://doi.org/10.1080/09658211.2017.1340483

Baddeley, A. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Sciences*, *4*(11), 417–423.

Baddeley, A., Eysenck, M. W., & Anderson, M. C. (2009). *Memory.* Psychology Press.

Baddeley, A. D. & Hitch, G. J. (1974) Working memory. In The Psychology of Learning and Motivation (Bower, G.A., ed.), pp. 47–89, Academic Press

Barker, A. T., Jalinous, R., & Freeston, I. L. (1985). Non-invasive magnetic stimulation of human motor cortex. *Lancet*, *1*(8437), 1106–1107. https://doi.org/10.1016/s0140-6736(85)92413-4

Barry, D. N., Barnes, G. R., Clark, I. A., & Maguire, E. A. (2019). The neural dynamics of novel scene imagery. *BioRxiv*, *39*(22), 4375–4386. https://doi.org/10.1101/429274

Bartlett, F.C. (1932). Remembering: A study in experimental and social psychology. Cambridge, UK: Cambridge University Press.

Bartolomeo, P., Hajhajate, D., Liu, J., & Spagna, A. (2020). Assessing the causal role of early visual areas in visual mental imagery. *Nature Reviews Neuroscience*, *59*, 2020. https://doi.org/10.1038/s41583-020-0348-5

Bazsaki, G. (2002). Theta Oscillations in the Hippocampus. *Neuron*, *33*, 325–340.

Benjamini, Y., & Hochberg. Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: series B (Methodological), 57*(1), 289-300.

Berens, S. C., & Horner, A. J. (2017). Theta Rhythm: Temporal Glue for Episodic Memory. *Current Biology*, *27*(20), R1110–R1112. https://doi.org/10.1016/j.cub.2017.08.048

Bergmann, T. O., Karabanov, A., Hartwigsen, G., Thielscher, A., & Siebner, H. R. (2016). Combining non-invasive transcranial brain stimulation with neuroimaging and electrophysiology: Current approaches and future perspectives. *NeuroImage*, *140*, 4–19. https://doi.org/10.1016/j.neuroimage.2016.02.012

Berryhill, M. E., Phuong, L., Picasso, L., Cabeza, R., & Olson, I. R. (2007). Parietal lobe and episodic memory: bilateral damage causes impaired free recall of autobiographical memory. *Journal of Neuroscience*, *27*(52), 14415–14423. https://doi.org/10.1523/JNEUROSCI.4163-07.2007

Berryhill, M. E., Picasso, L., Arnold, R., Drowos, D., & Olson, I. R. (2010). Similarities and differences between parietal and frontal patients in autobiographical and constructed experience tasks. *Neuropsychologia*, *48*(5), 1385–1393. https://doi.org/10.1016/j.neuropsychologia.2010.01.004

Bigelow, J., & Poremba, A. (2014). Achilles' ear? Inferior human short-term and recognition memory in the auditory modality. *PLoS ONE*, *9*(2). https://doi.org/10.1371/journal.pone.0089914

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

Blajenkova, O., Kozhevnikov, M., & Motes, M. A. (2006). Object-spatial imagery: A new self-report imagery questionnaire. *Applied Cognitive Psychology*, *20*(2), 239–263. https://doi.org/10.1002/acp.1182

Blazhenkova, O. (2016). Vividness of object and spatial imagery. *Perceptual and Motor Skills*, *122*(2), 490–508. https://doi.org/10.1177/0031512516639431

Bonnici, H. M., Richter, F. R., Yazar, Y., & Simons, J. S. (2016). Multimodal Feature Integration in the Angular Gyrus during Episodic and Semantic Retrieval. *Journal of Neuroscience*, *36*(20), 5462–5471. https://doi.org/10.1523/JNEUROSCI.4310-15.2016

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

Bonnici, H. M., Cheke, L. G., Green, D. A. E., FitzGerald, T. H. B., & Simons, J. S. (2018). Specifying a causal role for angular gyrus in autobiographical memory. *Journal of Neuroscience*, 1–16.

Brady, T. F., Konkle, T., Alvarez, G. A., & Oliva, A. (2008). Visual long-term memory has a massive storage capacity for object details. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(38), 14325–14329. https://doi.org/10.1073/pnas.0803390105

Bridge, H., Harrold, S., Holmes, E. A., Stokes, M., & Kennard, C. (2012). Vivid visual mental imagery in the absence of the primary visual cortex. *Journal of Neurology*, *259*(6), 1062–1070. https://doi.org/10.1007/s00415-011-6299-z

Buccino, G., Sato, M., Cattaneo, L., Rodà, F., & Riggio, L. (2009). Broken affordances, broken objects: a TMS study. *Neuropsychologia*, *47*(14), 3074–3078. https://doi.org/10.1016/j.neuropsychologia.2009.07.003

Buckner, R. L., & Wheeler, M. E. (2001). The cognitive neuroscience of remembering. *Nature Reviews Neuroscience*, *2*, 624–634.

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. https://doi.org/10.1017/S0048577200981356

Burgess, A. P., & Ali, L. (2002). Functional connectivity of gamma EEG activity is modulated at low frequency during conscious recollection. *International Journal of Psychophysiology*, *46*(2), 91–100. https://doi.org/10.1016/S0167-8760(02)00108-3

Burke, J. F., Sharan, A. D., Sperling, M. R., Ramayya, A. G., Evans, J. J., Healey, M. K., Beck, E. N., Davis, K. A., Lucas, T. H., & Kahana, M. J. (2014). Theta and high-frequency activity mark spontaneous recall of episodic memories. *Journal of Neuroscience*, *34*(34), 11355–11365. https://doi.org/10.1523/JNEUROSCI.2654-13.2014

Butler, A. C., Rice, H. J., Wooldridge, C. L., & Rubin, D. C. (2016). Visual imagery in autobiographical memory: The role of repeated retrieval in shifting perspective. *Consciousness and Cognition*, *42*, 237–253. https://doi.org/10.1016/j.concog.2016.03.018

Cabeza, R., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2008). The parietal cortex and episodic memory: an attentional account. *Nature Reviews. Neuroscience*, *9*(8), 613–625. https://doi.org/10.1038/nrn2459

Carbon, C. C., & Albrecht, S. (2012). Bartlett's schema theory: The unreplicated "portrait d'homme" series from 1932. *Quarterly Journal of Experimental Psychology*, *65*(11), 2258–2270. https://doi.org/10.1080/17470218.2012.696121

Caspers, S., Geyer, S., Schleicher, A., Mohlberg, H., Amunts, K., & Zilles, K. (2006). The human inferior parietal cortex: Cytoarchitectonic parcellation and interindividual variability. *NeuroImage*, *33*(2), 430–448. https://doi.org/10.1016/j.neuroimage.2006.06.054

Cheke, L. G., & Clayton, N. S. (2013). Do different tests of episodic memory produce consistent results in human adults? *Learning and Memory*, *20*(9), 491–498. https://doi.org/10.1101/lm.030502.113

Ciaramelli, E., Faggi, G., Scarpazza, C., Mattioli, F., Spaniol, J., Ghetti, S., & Moscovitch, M. (2017). Subjective recollection independent from multifeatural context retrieval following damage to the posterior parietal cortex. *Cortex*, *91*, 114–125. https://doi.org/10.1016/j.cortex.2017.03.015

Ciaramelli, E., Rosenbaum, R. S., Solcz, S., Levine, B., & Moscovitch, M. (2010). Mental space travel: Damage to posterior parietal cortex prevents egocentric navigation and reexperiencing of remote spatial memories. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *36*(3), 619–634. https://doi.org/10.1037/a0019181

Clemens, A. (2018, August 1). *When the mind's eye is blind*. Scientific American. https://www.scientificamerican.com/article/when-the-minds-eye-is-blind1/

Cohen, J. (1988). *Statistical power analysis for the social science (2^{nd}. Edition).* Hillsdale, New Jersey; Lawrence Erlbaum Associates.

Cohen, M.X. (2014) *Analyzing neural time series data: Theory and practice*, MIT press.

Cohen, M., Horowitz, T., & Wolfe, J. (2009). Auditory recognition memory is inferior to visual recognition memory. *PNAS*, *106*(14), 6008–6010. https://doi.org/10.1073/pnas.0811884106

Cohen, S. S., & Parra, L. C. (2016). Memorable audiovisual narratives synchronize sensory and supramodal neural responses. *ENeuro*, *3*(December), 1–11. https://doi.org/10.1523/ENEURO.0203-16.2016

Cohen, Y. E., Russ, B. E., & Gifford, G. W., 3rd (2005). Auditory processing in the posterior parietal cortex. *Behavioral and cognitive neuroscience reviews*, *4*(3), 218–231. https://doi.org/10.1177/1534582305285861

Colombo, M., & D'Amato, M. R. (1986). A Comparison of Visual and Auditory Short-Term Memory in Monkeys 'Cebus Apella.' *The Quarterly Journal of Experimental Psychology Section B*, *38*(4b), 425–448. https://doi.org/10.1080/14640748608402244

Conway, M. A. (2001). Sensory-perceptual episodic memory and its context: autobiographical memory. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *356*(1413), 1375–1384. https://doi.org/10.1098/rstb.2001.0940

Conway, M. A., & Pleydell-Pearce, C. W. (2000). The construction of autobiographical memories in the self-memory system. *Psychological review*, *107*(2), 261.

Conway, M. A, Pleydell-Pearce, C. W., Whitecross, S., & Sharpe, H. (n.d.). *Brain imaging autobiographical memory*. *41*.

Craik, F. I., Govoni, R., Naveh-Benjamin, M., & Anderson, N. D. (1996). The effects of divided attention on encoding and retrieval processes in human memory. *Journal of Experimental Psychology: General, 125*(2), 159-180.

Crutch, S., Lehmann, M., Schott, J. M., Rabinovici, G. D., Rossor, M. N., & Fox, N. C. (2012). Posterior cortical atrophy. *Lancet Neurology*, *11*(2), 170–178. https://doi.org/10.1016/S1474-4422(11)70289-7.

Cumming, J., & Eaves, D. L. (2018). The Nature, Measurement, and Development of Imagery Ability. *Imagination, Cognition and Personality*, *February*, 027623661775243. https://doi.org/10.1177/0276236617752439

D'Argembeau, A., & Van der Linden, M. (2006). Individual differences in the phenomenology of mental time travel: The effect of vivid visual imagery and emotion regulation strategies. *Consciousness and Cognition*, *15*(2), 342–350. https://doi.org/10.1016/j.concog.2005.09.001

Damasio, A.R. (1989). The brain binds entities and events by multiregional activation from convergence zones. *Neural Computation, 1*, 123-132.

Davidson, P. S. R., Anaki, D., Ciaramelli, E., Cohn, M., Kim, A. S. N., Murphy, K. J., Troyer, A. K., Moscovitch, M., & Levine, B. (2008). Does lateral parietal cortex support episodic memory?. Evidence from focal lesion patients. *Neuropsychologia*, *46*(7), 1743–1755. https://doi.org/10.1016/j.neuropsychologia.2008.01.011

Dawes, A. J., Keogh, R., Andrillon, T., & Pearson, J. (2020). A cognitive profile of multi-sensory imagery, memory and dreaming in aphantasia. *Scientific Reports*, *10*(1), 1–10. https://doi.org/10.1038/s41598-020-65705-7

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

Driediger, M., Hall, C., & Callow, N. (2006). Imagery use by injured athletes: A qualitative analysis. *Journal of Sports Sciences, 24*(3), 261-272. https://doi.org/10.1080/02640410500128221

Ebbinghaus, H. (1885). Memory: A contribution to experimental psychology. (Henry A Ruger & Calara E. Bussenius, Trad.). Original publicado em New York: Teachers College, Columbia University. (Original em alemão "Über das Gedächtnis", publicado em).

Eichenbaum, H. (2014). Time cells in the hippocampus: A new dimension for mapping memories. *Nature Reviews Neuroscience*, *15*(11), 732–744. https://doi.org/10.1038/nrn3827.

Farah, M. J. (1989). Mechanisms of imagery-perception interaction. *Journal of Experimental Psychology: Human Perception and Performance, 15*(2), 203–211. https://doi.org/10.1037/0096-1523.15.2.203

Farah, M. J., Hammond, K. M., Levine, D. N., & Calvanio, R. (1988). Visual and spatial mental imagery: Dissociable systems of representation. *Cognitive Psychology, 20*, 439–462. doi:10.1016/ 0010-0285(88)90012-6

Fell, J., & Axmacher, N. (2011). The role of phase synchronization in memory processes. *Nature Reviews Neuroscience*, *12*(2), 105–118. https://doi.org/10.1038/nrn2979

Fries, P. (2005). A mechanism for cognitive dynamics: Neuronal communication through neuronal coherence. *Trends in Cognitive Sciences*, *9*(10), 474–480. https://doi.org/10.1016/j.tics.2005.08.011

Fritsch, G., & Hitzig, E. (1870). Über die elekrische erregbarkeit des grosshirns. Arch. Anat. Physiol. Wissen. 37, 300–332

Fuentemilla, L., Barnes, G. R., Düzel, E., & Levine, B. (2014). Theta oscillations orchestrate medial temporal lobe and neocortex in remembering autobiographical memories. *NeuroImage*, *85*, 730–737. https://doi.org/10.1016/j.neuroimage.2013.08.029

Galton, F. (1880). Statistics of mental imagery. *Mind*, *5*(19), 301-318.

Gardiner, J. M. (2001). Episodic memory and autonoetic consciousness: A first-person approach. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *356*(1413), 1351–1361. https://doi.org/10.1098/rstb.2001.0955

Gevins, A., & Smith, M. E. (2000). Neurophysiological measures of working memory and individual differences in cognitive ability and cognitive style. *Cerebral cortex, 10*(9), 829–839. https://doi.org/10.1093/cercor/10.9.829

Gilboa, A. (2004). Autobiographical and episodic memory - One and the same? Evidence from prefrontal activation in neuroimaging studies. *Neuropsychologia*, *42*(10), 1336–1349. https://doi.org/10.1016/j.neuropsychologia.2004.02.014

Grafman, J., and Wassermann, E. (1998). Transcranial magnetic stimulation can measure and modulate learning and memory. *Neuropsychologia, 37*(2), 159–167.

Greenberg, D. L., & Knowlton, B. J. (2014). The role of visual imagery in autobiographical memory. *Memory & Cognition*, *42*(6), 922–934. https://doi.org/10.3758/s13421-014-0402-5

Greenberg, D. L., & Rubin, D. C. (2003). The neuropsychology of autobiographical memory. *Cortex, 39*, 687-728.

Gruber, T., & Müller, M. M. (2006). Oscillatory brain activity in the human EEG during indirect and direct memory tasks. *Brain Research*. https://doi.org/10.1016/j.brainres.2006.04.069

Guderian, S., & Düzel, E. (2005). Induced theta oscillations mediate large-scale synchrony with mediotemporal areas during recollection in humans. *Hippocampus*, *15*(7), 901–912. https://doi.org/10.1002/hipo.20125

Guyon, N., Zacharias, L. R., Oliveira, E. F. De, Kim, H., Leite, P., Lopes-Aguiar, C., Institutet, K., Sciences, B., Institutet, K., de Oliveira, E. F., Kim, H., Leite, J. P., Lopes-Aguiar, C., & Carlén, M. (2020). Network asynchrony underlying increased broadband gamma power. *BioRxiv*, 2020.08.26.265439. https://doi.org/10.1101/2020.08.26.265439

Hallett, M. (2007). Transcranial magnetic stimulation: a primer. *Neuron* 55, 187–199. doi: 10.1016/j.neuron.2007.06.026

Halpern, A. R. (2015). Differences in auditory imagery self-report predict neural and behavioral outcomes. *Psychomusicology: Music, Mind, and Brain*, *25*(1), 37–47. https://doi.org/10.1037/pmu0000081

Hanslmayr, S., Staresina, B. P., & Bowman, H. (2016). Oscillations and Episodic Memory: Addressing the Synchronization/Desynchronization Conundrum. *Trends in Neurosciences*, *39*(1), 16–25. https://doi.org/10.1016/j.tins.2015.11.004

Hanslmayr, S., & Staudigl, T. (2014). How brain oscillations form memories - A processing based perspective on oscillatory subsequent memory effects. *NeuroImage*, *85*, 648–655. https://doi.org/10.1016/j.neuroimage.2013.05.121

Hanslmayr, S., Staudigl, T., Aslan, A., & Bäuml, K. H. (2010). Theta oscillations predict the detrimental effects of memory retrieval. *Cognitive, Affective and Behavioral Neuroscience*, *10*(3), 329–338. https://doi.org/10.3758/CABN.10.3.329

Hanslmayr, S., Staudigl, T., & Fellner, M.-C. (2012). Oscillatory power decreases and long-term memory: the information via desynchronization hypothesis.

Frontiers in Human Neuroscience, *6*(April), 74. https://doi.org/10.3389/fnhum.2012.00074

Hassabis, D., Kumaran, D., Vann, S. D., & Maguire, E. A. (2007). Patients with hippocampal amnesia cannot imagine new experiences. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(5), 1726–1731. https://doi.org/10.1073/pnas.0610561104

Hassabis, D., & Maguire, E. A. (2009). The construction system of the brain. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1521), 1263–1271. https://doi.org/10.1098/rstb.2008.0296

Herrmann, C. S., Munk, M. H., & Engel, A. K. (2004). Cognitive functions of gamma-band activity: memory match and utilization. *Trends in cognitive sciences*, *8*(8), 347–355. https://doi.org/10.1016/j.tics.2004.06.006

Herrmann, C. S., Strüber, D., Helfrich, R. F., & Engel, A. K. (2016). EEG oscillations: From correlation to causality. *International Journal of Psychophysiology*, *103*, 12–21. https://doi.org/10.1016/j.ijpsycho.2015.02.003

Holmes, E. A., & Mathews, A. (2010). Mental imagery in emotion and emotional disorders. *Clinical Psychology Review*, *30*(3), 349–362. https://doi.org/10.1016/j.cpr.2010.01.001

Hower, K., Wixted, J., Berryhill, M., & OLson, I. R. (2014). *Impaired perception of mnemonic oldness, but not mnemonic newness*. *56*, 409–417. https://doi.org/10.1016/j.neuropsychologia.2014.02.014.

Huang, Y. Z., Edwards, M. J., Rounis, E., Bhatia, K. P., & Rothwell, J. C. (2005). Theta burst stimulation of the human motor cortex. *Neuron*, *45*(2), 201–206. https://doi.org/10.1016/j.neuron.2004.12.033

Humphreys, G. F., Ralph, M. A. L., & Simons, J. S. (n.d.). *A Unifying Account of Angular Gyrus Contributions to Episodic and Semantic Cognition*. 1–21.

Irish, M., Halena, S., Kamminga, J., Tu, S., Hornberger, M., & Hodges, J. R. (2015). Scene construction impairments in Alzheimer's disease - A unique role for the posterior cingulate cortex. *Cortex*, *73*, 10–23. https://doi.org/10.1016/j.cortex.2015.08.004

Irish, M., Lawlor, B. A., O'Mara, S. M., & Coen, R. F. (2011). Impaired capacity for autonoetic reliving during autobiographical event recall in mild Alzheimer's disease. *Cortex*, *47*(2), 236–249. https://doi.org/10.1016/j.cortex.2010.01.002

Jacobs, J., Hwang, G., Curran, T., & Kahana, M. J. (2006). EEG oscillations and recognition memory: Theta correlates of memory retrieval and decision making. *NeuroImage*, *32*(2), 978–987. https://doi.org/10.1016/j.neuroimage.2006.02.018

James, W., 1890. The principles of Psychology: Pantianos Classics.

Jensen, A. R. (1971). Individual differences in visual and auditory memory. *Journal of Educational Psychology*, *62*(2), 123–131. https://doi.org/10.1037/h0030655

Jonker, T. R., Dimsdale-Zucker, H., Ritchey, M., Clarke, A., & Ranganath, C. (2018). Neural reactivation in parietal cortex enhances memory for episodically linked information. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(43), 11084–11089. https://doi.org/10.1073/pnas.1800006115

Johnson, M. K., Suengas, A. G., Foley, M. A., & Raye, C. L. (1988). Phenomenal characteristics of memories for perceived and imagined memories autobiographical events. *Journal of Experimental Psychology: General, 117*, 371-376.

Jung, J., Bungert, A., Bowtell, R., & Jackson, S. R. (2016). Vertex Stimulation as a Control Site for Transcranial Magnetic Stimulation: A Concurrent TMS/fMRI Study. *Brain Stimulation*, *9*(1), 58–64. https://doi.org/10.1016/j.brs.2015.09.008

Kahana, M. J., Seelig, D., & Madsen, J. R. (2001). Theta returns. *Current Opinion in Neurobiology*, *11*, 739–744.

Karakaş, S., & Barry, R. J. (2017). A brief historical perspective on the advent of brain oscillations in the biological and psychological disciplines. *Neuroscience & Biobehavioral Reviews*, *75*(266), 335–347. https://doi.org/10.1016/j.neubiorev.2016.12.009

Keogh, R., & Pearson, J. (2017). The perceptual and phenomenal capacity of mental imagery. *Cognition*, *162*, 124–132. https://doi.org/10.1016/j.cognition.2017.02.004

Keogh, R., & Pearson, J. (2017). The blind mind: No sensory visual imagery in aphantasia. *Cortex*, *2015*, 1–8. https://doi.org/10.1016/j.cortex.2017.10.012

Khader, P. H., & Rösler, F. (2011). EEG power changes reflect distinct mechanisms during long-term memory retrieval. *Psychophysiology*, *48*(3), 362–369. https://doi.org/10.1111/j.1469-8986.2010.01063.x

Klimesch, W. (1996). Memory processes, brain oscillations and EEG synchronization. *International Journal of Psychophysiology*. https://doi.org/10.1016/S0167-8760(96)00057-8

Klimesch, W. (1997). EEG-alpha rhythms and memory processes. *International Journal of Psychophysiology*. https://doi.org/10.1016/S0167-8760(97)00773-3

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a rKlimesch, 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/S016. *Brain Research Reviews*, *29*(2–3), 169–195. https://doi.org/10.1016/S0165-0173(98)00056-3

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. https://doi.org/10.1016/j.brainres.2008.06.049

Klimesch, W., Hanslmayr, S., Sauseng, P., Gruber, W., Brozinsky, C. J., Kroll, N. E. A., Yonelinas, A. P., & Doppelmayr, M. (2006). Oscillatory EEG correlates of episodic trace decay. *Cerebral Cortex*, *16*(2), 280–290. https://doi.org/10.1093/cercor/bhi107

Klimesch, W., Pfurtscheller, G., & Schimke, H. (1992). Pre-and post-stimulus processes in category judgement tasks as measured by event-related desynchronization (ERD). *Journal of Psychophysiology*.

Klimesch, W., Schimke, H., & Schwaiger, J. (1994). Episodic and semantic memory: an analysis in the EEG theta and alpha band. *Electroencephalography and Clinical Neurophysiology*. https://doi.org/10.1016/0013-4694(94)90164-3

Kojima, S. (1985). Auditory short-term memory in the Japanese monkey. *International Journal of Neuroscience*, *25*(3-4), 255-262.

Kosslyn, S. M., Ganis, G., Thompson, W. L., & Hall, W. J. (2001). Kosslyn, S. M., Ganis, G., Thompson, W. L. (2001). Neural foundations of imagery. *Nature Reviews Neuroscienc*e, 2(9), 635.

Kosslyn, S. M. (1981). The medium and the message in mental imagery: A theory. *Psychological Review*. https://doi.org/10.1037/0033-295X.88.1.46

Kosslyn, S. M., Thompson, W. L., & Ganis, G. (2006). *The case for mental imagery.* Oxford University Press. https://doi.org/10.1093/acprof:oso/9780195179088.001.0001

Lawrence, M. (2020, April 1). *'I have no mind's eye': What it is it like being an author with aphantasia*? The Guardian. https://www.theguardian.com/books/2020/apr/01/being-an-author-with-aphantasia-mark-lawrence

Lega, B., Burke, J., Jacobs, J., & Kahana, M. J. (2016). Slow-Theta-to-Gamma Phase-Amplitude Coupling in Human Hippocampus Supports the Formation of New Episodic Memories. *Cerebral Cortex*, *26*(1), 268–278. https://doi.org/10.1093/cercor/bhu232

LePort, A. K. R., Mattfeld, A. T., Dickinson-Anson, H., Fallon, J. H., Stark, C. E. L., Kruggel, F., Cahill, L., & McGaugh, J. L. (2012). Behavioral and neuroanatomical investigation of highly superior autobiographical memory (HSAM). *Neurobiol Lean Mem*, *98*(1), 78–92. https://doi.org/10.1016/j.nlm.2012.05.002

LePort, A. K. R., Stark, S. M., McGaugh, J. L., & Stark, C. E. L. (2017). A cognitive assessment of highly superior autobiographical memory. *Memory*, *25*(2), 276–288. https://doi.org/10.1080/09658211.2016.1160126

Levine, B., Svoboda, E., Hay, J. F., Winocur, G., & Moscovitch, M. (2002). Aging and autobiographical memory: Dissociating episodic from semantic retrieval. *Psychology and Aging*, *17*(4), 677–689. https://doi.org/10.1037/0882-7974.17.4.677

Logie, R. H. (2003). Spatial and Visual Working Memory: A Mental Workspace. *Psychology of Learning and Motivation - Advances in Research and Theory*. https://doi.org/10.1016/S0079-7421(03)01002-8

Long, N. M., Burke, J. F., & Kahana, M. J. (2014). Subsequent memory effect in intracranial and scalp EEG. *NeuroImage*, *84*, 488–494. https://doi.org/10.1016/j.neuroimage.2013.08.052

Luber, B., & Lisanby, S. H. (2014). Enhancement of human cognitive performance using transcranial magnetic stimulation (TMS). *Neuroimage, 15*, 961–970. doi: 10.1016/j.neuroimage.2013.06.007

Maguire, E. A., Intraub, H., & Mullally, S. L. (2016). Scenes, Spaces, and Memory Traces: What Does the Hippocampus Do? *Neuroscientist*, *22*(5), 432–439. https://doi.org/10.1177/1073858415600389

Maguire, E. A., & Mullally, S. L. (2013). The hippocampus: A manifesto for change. *Journal of Experimental Psychology: General*, *142*(4), 1180–1189. https://doi.org/10.1037/a0033650

Mahr, J. B., & Csibra, G. (2018). Why do we remember? the communicative function of episodic memory. *Behavioral and Brain Sciences*, *41*, 1–16. https://doi.org/10.1017/S0140525X17000012

Makeig, S. (1993). Auditor-Event-Related Dynamics of the EEG Spectrum. *Electroencephalography and Clinical Neurophysiology*, *86*, 20. https://sccn.ucsd.edu/~scott/pdf/ERSP93.pdf%0Apapers2://publication/uuid/03A98A40-49C2-4E7A-A91F-B4E0D2B98237

Makeig, S., Debener, S., Onton, J., & Delorme, A. (2004). Mining event-related brain dynamics. *Trends in cognitive sciences*, *8*(5), 204–210. https://doi.org/10.1016/j.tics.2004.03.008

Mandler, G. (1980). Recognizing: The judgment of previous occurrence. *Psychological Review, 87*(3), 252–271. https://doi.org/10.1037/0033-295X.87.3.252

Manenti, R., Cotelli, M., Robertson, I. H., & Miniussi, C. (2012). Transcranial brain stimulation studies of episodic memory in young adults, elderly adults and individuals with memory dysfunction: A review. *Brain Stimulation*, *5*(2), 103–109. https://doi.org/10.1016/j.brs.2012.03.004

Marks, D. F. (1973). Visual imagery differences in the recall of pictures. *British Journal of Psychology*, *64*(1), 17–24.

Martin, C. D., Baudouin, J. Y., Franck, N., Guillaume, F., Guillem, F., Huron, C., & Tiberghien, G. (2011). Comparison of RK and confidence judgement ROCs in recognition memory. *Journal of Cognitive Psychology*, *23*(2), 171–184. https://doi.org/10.1080/20445911.2011.476722

Mathôt, S., Schreij, D., & Theeuwes, J. (2012). OpenSesame: An open-source, graphical experiment builder for the social sciences. *Behavior Research Methods, 44*(2), 314-324. doi:10.3758/s13428-011-0168-7

Matusz, P. J., Thelen, A., Amrein, S., Geiser, E., Anken, J., & Murray, M. M. (2015). The role of auditory cortices in the retrieval of single-trial auditory-visual object memories. *European Journal of Neuroscience*, *41*(5), 699–708. https://doi.org/10.1111/ejn.12804

Mazard, A. L., Tzourio-Mazoyer, N., Crivello, F., Mazoyer, B., & Mellet, E. (2004). A PET meta-analysis of object and spatial mental imagery. *European Journal of Cognitive Psychology, 16*, 673–695. doi:10.1080/09541440340000484

Mickes, L., Wais, P. E., & Wixted, J. T. (2009). Recollection is a continuous process: Implications for dual-process theories of recognition memory. *Psychological Science, 20*, 509e515.

Miniussi, C., & Thut, G. (2010). Combining TMS and EEG offers new prospects in cognitive neuroscience. *Brain Topography*, *22*(4), 249–256. https://doi.org/10.1007/s10548-009-0083-8

Morgan, H. M., Muthukumaraswamy, S. D., Hibbs, C. S., Shapiro, K. L., Bracewell, R. M., Singh, K. D., & Linden, D. E. J. (2011). Feature integration in visual working memory: parietal gamma activity is related to cognitive coordination. *Journal of Neurophysiology*, *106*, 3185–3194. https://doi.org/10.1152/jn.00246.2011.

Moro, V., Berlucchi, G., Lerch, J., Tomaiuolo, F., & Aglioti, S. M. (2008). Selective deficit of mental visual imagery with intact primary visual cortex and visual perception. *Cortex*, *44*(2), 109–118. https://doi.org/10.1016/j.cortex.2006.06.004

Moscovitch, M., Cabeza, R., Winocur, G., & Nadel, L. (2016). Episodic memory and beyond: The hippocampus and neocortex in transformation. *Annual Review of Psychology*, *67*(1), 105–134. https://doi.org/10.1146/annurev-psych-113011-143733

Mullally, S. L., Intraub, H., & Maguire, E. A. (2012). Attenuated boundary extension produces a paradoxical memory advantage in amnesic patients. *Current Biology*, *22*(4), 261–268. https://doi.org/10.1016/j.cub.2012.01.001

Mullally, S. L., Vargha-Khadem, F., & Maguire, E. A. (2014). Scene construction in developmental amnesia: An fMRI study. *Neuropsychologia*, *52*(1), 1–10. https://doi.org/10.1016/j.neuropsychologia.2013.11.001

Murdock, B.B. (1985). The contributions of Hermann Ebbinghaus. *Journal of Experimental Psychology: Memory, and Cognition, 11*(3), 469-471. https://doi.org/10.1037/0278-7393.11.3.469

Navarra, J., Alsius, A., Soto-Faraco, S., & Spence, C. (2010). Assessing the role of attention in the audiovisual integration of speech. *Information Fusion*, *11*(1), 4–11. https://doi.org/10.1016/j.inffus.2009.04.001

Nitsche, M.A., Cohen, L.G., Wassermann, E.M., Priori, A., Lang. N., Antal, A., … & Pascual-Leone, A. (2008). Transcranial direct current stimulation: State of the art 2008. *Brain Stimulation, 1*(3), 206-223.

Noble, W. S. (2009). How Does Multiple Testing Correction Work? *Nature Biotechnology*, *27*(12), 1135–1137. https://doi.org/10.1038/nbt1209-1135.

Norman, K. A. (2010). How hippocampus and cortex contribute to recognition memory: Revisiting the complementary learning systems model. *Hippocampus, 20,* 1217e1227.

Nyhus, E., & Curran, T. (2010). Functional role of gamma and theta oscillations in episodic memory. *Neuroscience and Biobehavioral Reviews*, *34*(7), 1023–1035. https://doi.org/10.1016/j.neubiorev.2009.12.014

Olsen, R. K., Moses, S. N., Riggs, L., & Ryan, J. D. (2012). The hippocampus supports multiple cognitive processes through relational binding and comparison. *Frontiers in Human Neuroscience*, *6*(MAY 2012), 1–13. https://doi.org/10.3389/fnhum.2012.00146

Palombo, D. J., Alain, C., Söderlund, H., Khuu, W., & Levine, B. (2015). Severely deficient autobiographical memory (SDAM) in healthy adults: A new mnemonic syndrome. *Neuropsychologia*, *72*, 105–118. https://doi.org/10.1016/j.neuropsychologia.2015.04.012

Paivio, A. (1971). Imagery and language. In *Imagery* (pp. 7-32). Academic Press.

Pascual-Leone, A., Tormos, J. M., Keenan, J., Tarazona, F., Cañete, C., & Catalá, M. D. (1998). Study and modulation of human cortical excitability with transcranial magnetic stimulation. *Journal of Clinical Neurophysiology, 15*(4), 333-343.

Pearson, J. (2014). New directions in mental-imagery research: The binocular-rivalry technique and decoding fMRI patterns. Current Directions in Psychological Science, 23(3), 178e183. https:// doi.org/10.1177/0963721414532287.

Pearson, J., & Kosslyn, S. M. (2015). The heterogeneity of mental representation: Ending the imagery debate. *Proceedings of the National Academy of Sciences*, *112*(33), 10089–10092. https://doi.org/10.1073/pnas.1504933112

Pearson, J., Naselaris, T., Holmes, E. A., & Kosslyn, S. M. (2015). Mental Imagery: Functional Mechanisms and Clinical Applications. *Trends in Cognitive Sciences*, *19*(10), 590–602. https://doi.org/10.1016/j.tics.2015.08.003

Pylyshyn, Z. (2003). Return of the mental image: Are there really pictures in the brain? *Trends in Cognitive Sciences*, *7*(3), 113–118. https://doi.org/10.1016/S1364-6613(03)00003-2

Pfurtscheller, G., & Aranibar, A. (1977). Event-related cortical desynchronization detected by power measurements of scalp EEG. Electroencephalography and Clinical Neurophysiology, 42(6), 817e826.

Pfurtscheller, G., & Lopes Da Silva, F. H. (1999). Event-related EEG/MEG synchronization and desynchronization: Basic principles. In *Clinical Neurophysiology*. https://doi.org/10.1016/S1388-2457(99)00141-8

Pfurtscheller, G., & Neuper, C. (1997). Motor imagery activates primary sensorimotor area in humans. *Neuroscience Letters*. https://doi.org/10.1016/S0304-3940(97)00889-6

Quak, M., London, R. E., & Talsma, D. (2015). A multisensory perspective of working memory. *Frontiers in Human Neuroscience*, *9*(April), 197. https://doi.org/10.3389/fnhum.2015.00197

Raby, C. R., & Clayton, N. S. (2012). Episodic Memory and Planning. In *The Oxford Handbook of Comparative Evolutionary Psychology* (Issue January). https://doi.org/10.1093/oxfordhb/9780199738182.013.0012

Ramanan, S., Alaeddin, S., Goldberg, Z. lee, Strikwerda-Brown, C., Hodges, J. R., & Irish, M. (2018). Exploring the contribution of visual imagery to scene construction – Evidence from Posterior Cortical Atrophy. *Cortex*, *106*, 261–274. https://doi.org/10.1016/j.cortex.2018.06.016

Ramanan, S., Piguet, O., & Irish, M. (2018). Rethinking the Role of the Angular Gyrus in Remembering the Past and Imagining the Future: The Contextual Integration Model. *Neuroscientist*, *24*(4), 342–352. https://doi.org/10.1177/1073858417735514

Renoult, L., Davidson, P. S. R., Schmitz, E., Park, L., Campbell, K., Moscovitch, M., & Levine, B. (2014). Autobiographical significant concepts: More episodic than semantic in nature? An electrophysiological investigation of overlapping types of memory. *Journal of Cognitive Neuroscience*, *27*(1), 57–72. https://doi.org/10.1162/jocn_a_00689

Renoult, L., Davidson, P. S. R., Palombo, D. J., Moscovitch, M., & Levine, B. (2012). Personal semantics: At the crossroads of semantic and episodic memory. *Trends in Cognitive Sciences*, *16*(11), 550–558. https://doi.org/10.1016/j.tics.2012.09.003

Renoult, L., Irish, M., Moscovitch, M., & Rugg, M. D. (2019). From Knowing to Remembering: The Semantic–Episodic Distinction. *Trends in Cognitive Sciences*, *23*(12), 1041–1057. https://doi.org/10.1016/j.tics.2019.09.008

Renoult, L., & Rugg, M. D. (2020). An historical perspective on Endel Tulving's episodic-semantic distinction. *Neuropsychologia*, *139*(July 2019), 107366. https://doi.org/10.1016/j.neuropsychologia.2020.107366

Richardson, J. T. (1999). *Imagery*. Hove: Psychology Press.

Richter, F. R., Cooper, R. a, Bays, P. M., & Simons, J. S. (2016). Distinct neural mechanisms underlie the success, precision, and vividness of episodic memory. *ELife*, *5*, 1–18. https://doi.org/10.7554/eLife.18260

Rondina, R., 2nd, Olsen, R. K., McQuiggan, D. A., Fatima, Z., Li, L., Oziel, E., & Ryan, J. D. (2015). Age-related changes to oscillatory dynamics in hippocampal and neocortical networks. Neurobiology of Learning and Memory. http://dx.doi.org/10.1016/ j.nlm.2015.11.017.

Romero, M. C., Davare, M., Armendariz, M., & Janssen, P. (2019). Neural effects of transcranial magnetic stimulation at the single-cell level. *Nature Communications*, *10*(1), 1–11. https://doi.org/10.1038/s41467-019-10638-7

Rossi, S., Hallett, M., Rossini, P. M., & Pascual-Leone, A. (2009). Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. *Clinical Neurophysiology*, *120*(12), 323–330. https://doi.org/10.1016/j.clinph.2009.08.016.Rossi

Rubin, D. C. (2005). A basic-systems approach to autobiographical memory. *Current Directions in Psychological Science, 14*,79-83

Rubin, D. C., Burt, C. D. B., & Fifield, S. J. (2003). Experimental manipulations of the phenomenology of memory. *Memory and Cognition*, *31*(6), 877–886. https://doi.org/10.3758/BF03196442

Rubin, D. C., Schrauf, R. W., & Greenberg, D. L. (2003). Belief and recollection of autobiographical memories. *Memory and Cognition*, *31*(6), 887–901. https://doi.org/10.3758/BF03196443

Rubin, D. C., & Umanath, S. (2015). Event memory: A theory of memory for laboratory, autobiographical, and fictional events. *Psychological Review*, *122*(1), 1–23. https://doi.org/10.1037/a0037907

Rugg, M. D., & King, D. R. (2018). Ventral lateral parietal cortex and episodic memory retrieval. *Cortex*, *107*, 238–250. https://doi.org/10.1016/j.cortex.2017.07.012

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

Sack, A. T., Cohen Kadosh, R., Schuhmann, T., Moerel, M., Walsh, V., & Goebel, R. (2009). Optimizing Functional Accuracy of TMS in Cognitive Studies: A Comparison of Methods. *Journal of Cognitive Neuroscience*, *21*(2), 207–221. https://doi.org/10.1162/jocn.2009.21126

Santangelo, V., Van Der Lubbe, R. H. J., Olivetti Belardinelli, M., & Postma, A. (2008). Multisensory integration affects ERP components elicited by exogenous cues. *Experimental Brain Research*, *185*(2), 269–277. https://doi.org/10.1007/s00221-007-1151-5

Schacter, D. L., & Addis, D. R. (2009). On the nature of medial temporal lobe contributions to the constructive simulation of future events. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1521), 1245–1253. https://doi.org/10.1098/rstb.2008.0308

Seghier, M. L. (2013). The Angular Gyrus: Multiple Functions and Multiple Subdivisions. *The Neuroscientist*, *19*(1), 43–61. https://doi.org/10.1177/1073858412440596

Seghier, M. L., Fagan, E., & Price, C. J. (2010). Functional subdivisions in the left angular gyrus where the semantic system meets and diverges from the default network. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *30*(50), 16809–16817. https://doi.org/10.1523/JNEUROSCI.3377-10.2010

Sestieri, C., Capotosto, P., Tosoni, A., Luca Romani, G., & Corbetta, M. (2013). Interference with episodic memory retrieval following transcranial stimulation of the inferior but not the superior parietal lobule. *Neuropsychologia*, *51*(5), 900–906. https://doi.org/10.1016/j.neuropsychologia.2013.01.023

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

Shams, L., & Seitz, A. R. (2008). Benefits of multisensory learning. *Trends in Cognitive Sciences*, *12*(11), 411–417. https://doi.org/10.1016/j.tics.2008.07.006

Sheldon, S., & El-Asmar, N. (2018). The cognitive tools that support mentally constructing event and scene representations. *Memory*, *26*(6), 858–868. https://doi.org/10.1080/09658211.2017.1417440

Sheldon, S., Farb, N., Palombo, D. J., & Levine, B. (2016). Intrinsic medial temporal lobe connectivity relates to individual differences in episodic autobiographical remembering. *Cortex*, *74*, 206–216. https://doi.org/10.1016/j.cortex.2015.11.005

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

Simons, J. S., Peers, P. V., Hwang, D. Y., Ally, B. a., Fletcher, P. C., & Budson, A. E. (2008). Is the parietal lobe necessary for recollection in humans? *Neuropsychologia*, *46*(4), 1185–1191. https://doi.org/10.1016/j.neuropsychologia.2007.07.024

Simons, J. S., Peers, P. V., Mazuz, Y. S., Berryhill, M. E., & Olson, I. R. (2010). Dissociation between memory accuracy and memory confidence following bilateral parietal lesions. *Cerebral Cortex*, *20*(2), 479–485. https://doi.org/10.1093/cercor/bhp116

Smith, E. E., & Kosslyn, S. M. (2007). *Cognitive psychology: Mind and brain.* Upper Saddle River, NJ: Pearson Prentice Hall

Spiers, H. J., & Maguire, E. A. (2006). Thoughts, behaviour, and brain dynamics during navigation in the real world. *NeuroImage*, *31*(4), 1826–1840. https://doi.org/10.1016/j.neuroimage.2006.01.037

Squire, L. R. (1992). Declarative and nondeclarative memory: Multiple brain systems supporting learning and memory. *Journal of cognitive neuroscience*, *4*(3), 232-243.

Squire, L. R. (2009). The legacy of patient H.M. for neuroscience. *Neuron*, *15*(1), 6–9. https://doi.org/10.1016/j.neuron.2008.12.023

St. Jacques, P. L., & Levine, B. (2007). Ageing and autobiographical memory for emotional and neutral events. *Memory*, *15*(2), 129–144. https://doi.org/10.1080/09658210601119762

Standing, L. (1973). Learning 10,00 pictures. *Quarterly Journal of Experimental Psychology, 25*, 207–222.

Staudigl, T., & Hanslmayr, S. (2013). Theta oscillations at encoding mediate the context-dependent nature of human episodic memory. *Current Biology*, *23*(12), 1101–1106. https://doi.org/10.1016/j.cub.2013.04.074

Staudigl, T., Hanslmayr, S., & Bäuml, K. H. T. (2010). Theta oscillations reflect the dynamics of interference in episodic memory retrieval. *Journal of Neuroscience*, *30*(34), 11356–11362. https://doi.org/10.1523/JNEUROSCI.0637-10.2010

Stein, B. E., Burr, D., Constantinidis, C., Laurienti, P. J., Alex Meredith, M., Perrault, T. J., et al. (2010). Semantic confusion regarding the development of multisensory integration: a practical solution. *European Journal of Neuroscience, 31*(10), 1713–1720. doi: 10.1111/j.1460-9568.2010.07206.x

Steriade, M., & Llinas, R. R. (1988). The functional states of the thalamus and the associated neuronal interplay. In *Physiological Reviews*. https://doi.org/10.1152/physrev.1988.68.3.649

Strunk, J., James, T., Arndt, J., & Duarte, A. (2017). Age-related changes in neural oscillations supporting context memory retrieval. *Cortex*, *91*, 40–55. https://doi.org/10.1016/j.cortex.2017.01.020

Svoboda, E., McKinnon, M. C., & Levine, B. (2006). The functional neuroanatomy of autobiographical memory: A meta-analysis. *Neuropsychologia*, *44*(12), 2189–2208. https://doi.org/10.1016/j.neuropsychologia.2006.05.023

Tallon-Baudry, C., & Bertrand, O. (1999). Oscillatory gamma activity in humans and its role in object representation. In *Trends in Cognitive Sciences*. https://doi.org/10.1016/S1364-6613(99)01299-1

Tallon-Baudry, C., Bertrand, O., Peronnet, F., & Pernier, J. (1998). Induced γ-band activity during the delay of a visual short-term memory task in humans. *Journal of Neuroscience*. https://doi.org/10.1523/jneurosci.18-11-04244.1998

Talsma, D. (2015). Predictive coding and multisensory integration: an attentional account of the multisensory mind. *Frontiers in Integrative Neuroscience*, *9*(March), 19. https://doi.org/10.3389/fnint.2015.00019

Talsma, D., Senkowski, D., Soto-Faraco, S., & Woldorff, M. G. (2010). The multifacteted interplay between attention and multisensory integration. *Trends in Cognitive Sciences*, *14*(9), 400–410. https://doi.org/10.1016/j.tics.2010.06.008

Tang, X., Wu, J., & Shen, Y. (2016). The interactions of multisensory integration with endogenous and exogenous attention. *Neuroscience & Biobehavioral Reviews*, *61*, 208–224. https://doi.org/10.1016/j.neubiorev.2015.11.002

Thompson, W. L., Slotnick, S. D., Burrage, M. S., & Kosslyn, S. M. (2009). Two forms of spatial imagery: neuroimaging evidence. *Psychological science*, *20*(10), 1245–1253. https://doi.org/10.1111/j.1467-9280.2009.02440.x

Thut, G., & Miniussi, C. (2009). New insights into rhythmic brain activity from TMS-EEG studies. *Trends in Cognitive Sciences*, *13*(4), 182–189. https://doi.org/10.1016/j.tics.2009.01.004

Thut, G., Miniussi, C., & Gross, J. (2012). The functional importance of rhythmic activity in the brain. *Current Biology*, *22*(16), R658–R663. https://doi.org/10.1016/j.cub.2012.06.061

Tulving, E. (1972). Episodic and semantic memory. In: Organization of Memory. Academic Press, New York, pp. 381–403.

Tulving, E. (1983). Elements of Episodic Memory. Oxford University Press, New York.

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

Tulving, E. (2005). Episodic memory and autonoesis: uniquely human? In: Terrace, H.S., Metcalfe, J. (Eds.), The Missing Link in Cognition: Origins of Self-Reflective Consciousness. Oxford University Press, New York, pp. 3–56.

Turk, K. W., A., E. A., Deason, R. G., Heyworth, N. C., Nagle, C., Frustace, B., Flannery, S., Zumwalt, A., & Budson, A. E. (2018). Late positive component event-related potential amplitude predicts long-term classroom-based learning. *Journal of Cognitive Neuroscience*, *30*(9), 1323–1329. https://doi.org/10.1162/jocn_a_01285

Uddin, L.Q., Supekar, K., Amin, H., Rykhlevskaia, E., Nguyen, D.A., Greicius, M.D., & Menon, V. (2010). Dissociable connectivity within human angular gyrus and intraparietal sulcus: Evidence from functional and structureal connectivity. *Cerebral Cortex, 20*(11), 2636-2646.

Vannucci, M., Pelagatti, C., Chiorri, C., & Mazzoni, G. (2016). Visual object imagery and autobiographical memory: Object Imagers are better at remembering their personal past. *Memory*, *24*(4), 455–470. https://doi.org/10.1080/09658211.2015.1018277

Varela, F. J. (1995). Resonant cell assemblies: A new approach to cognitive function and neuronal synchrony. *Biological research, 28*, 81-95.

Varela, F., Lachaux, J. P., Rodriguez, E., & Martinerie, J. (2001). The brainweb: Phase synchronization and large-scale integration. *Nature Reviews Neuroscience*, *2*(4), 229–239. https://doi.org/10.1038/35067550

Vidal, J. R., Chaumon, M., O’Regan, J. K., & Tallon-Baudry, C. (2006). Visual grouping and the focusing of attention induce gamma-band oscillations at different frequencies in human magnetoencephalogram signals. *Journal of Cognitive Neuroscience*, *18*(11), 1850–1862. https://doi.org/10.1162/jocn.2006.18.11.1850

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

Villena-González, M., Palacios-García, I., Rodríguez, E., & López, V. (2018). Beta Oscillations Distinguish Between Two Forms of Mental Imagery While Gamma and Theta Activity Reflects Auditory Attention. *Frontiers in Human Neuroscience*, *12*(September), 1–11. https://doi.org/10.3389/fnhum.2018.00389

Visscher, K. M., Kaplan, E., Kahana, M. J., & Sekuler, R. (2007). Auditory short-term memory behaves like visual short-term memory. *PLoS Biology*, *5*(3), 0662–0672. https://doi.org/10.1371/journal.pbio.0050056

Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences*, *9*(9), 445–453. https://doi.org/10.1016/j.tics.2005.07.001

Wahn, B., & König, P. (2017). Is attentional resource allocation across sensory modalities task-dependent? *Advances in Cognitive Psychology*, *13*(1), 83–96. https://doi.org/10.5709/acp-0209-2

Waldhauser, G. T., Johansson, M., & Hanslmayr, S. (2012). Alpha/beta oscillations indicate inhibition of interfering visual memories. *Journal of Neuroscience*, *32*(6), 1953–1961. https://doi.org/10.1523/JNEUROSCI.4201-11.2012

Wang, Q., Hou, Y., Tang, H., & Wiprovnick, A. (2011). Travelling back- wards and forwards in time: Culture and gender in the episodic specificity of past and future events. Memory, 19, 103–109. doi:10.1080/09658211.2010.537279

Wassermann, E. M. (1998). Rish and safety of repetitive transcranial magnetic stimulation: Report and suggested guidelines from the International Workshop on the Safety of Repetitive Transcranial Magnetic Stimulation, June 5-7, 1996. *Electroencephalography and Clinical Neurophysiology/Evoked Potentional Section, 108*(1), 1-16.

Wheeler, M. A., Stuss, D. T., & Tulving, E. (1997). Toward a theory of episodic memory: The frontal lobes and autonoetic consciousness. In *Psychological Bulletin* (Vol. 121, Issue 3, pp. 331–354). https://doi.org/10.1037//0033-2909.121.3.331

Wheeler, M. E., Petersen, S. E., & Buckner, R. L. (2000). Memory ’ s echo : Vivid remembering reactivates sensory-specific cortex. *Pnas*, *97*(20), 11125–11129. https://doi.org/10.1073/pnas.97.20.11125

Wilson, B. A., & Wearing, D. (1995). *Prisoner of consciousness: A state of just awakening following herpes simplex encephalitis.* In R. Campbell & M. A. Conway (Eds.), *Broken memories: Case studies in memory impairment* (p. 14–30). Blackwell Publishing.

Wixted, J. T., & Mickes, L. (2010). A continuous dual-process model of remember/know judgments. *Psychological Review, 117*, 1025e1054.

Winlove, C. I. P., Milton, F., Ranson, J., Fulford, J., MacKisack, M., Macpherson, F., & Zeman, A. (2018). The neural correlates of visual imagery: A co-ordinate-based meta-analysis. *Cortex*, *105*, 4–25. https://doi.org/10.1016/j.cortex.2017.12.014

Wischnewski, M., & Schutter, D. J. (2015). Efficacy and Time Course of Theta Burst Stimulation in Healthy Humans. *Brain stimulation*, *8*(4), 685–692. https://doi.org/10.1016/j.brs.2015.03.004

Wood, H., & Byatt, A. S. (2009). *Memory: An anthology*. Vintage Books.

Yang, H., Laforge, G., Stojanoski, B., Nichols, E. S., McRae, K., & Köhler, S. (2019). Late positive complex in event-related potentials tracks memory signals when they are decision relevant. *Scientific Reports*, *9*(1), 1–15. https://doi.org/10.1038/s41598-019-45880-y

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

Yazar, Y., Bergström, Z. M., & Simons, J. S. (2014). Continuous theta burst stimulation of angular gyrus reduces subjective recollection. *PLoS ONE*, *9*(10). https://doi.org/10.1371/journal.pone.0110414

Yeh, N., & Rose, N. S. (2019). How can transcranial magnetic stimulation be used to modulate episodic memory?: A systematic review and meta-analysis. *Frontiers in Psychology*, *10*(JUN). https://doi.org/10.3389/fpsyg.2019.00993

Yu, S. S., Johnson, J. D., & Rugg, M. D. (2012). Dissociation of recollection-related neural activity in ventral lateral parietal cortex. *Cognitive Neuroscience, 3*(3-4), 142–149. https://doi.org/10.1080/17588928.2012.669363

Zeman, A., Dewar, M., & Della Sala, S. (2015). Lives without imagery - Congenital aphantasia. *Cortex*, *73*, 378–380. https://doi.org/10.1016/j.cortex.2015.05.019

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

Appendices

Appendix A: The Vividness of Visual Imagery Questionniare

For full details please see:
Marks (1973).

Please read the instructions below (*in italics*) and take a moment to visualise them. Once you have done this, read the descriptions **1-16** and tick the box that you feel represents that mental image you experience: Perfectly clear and as vivid as normal vision, clear and reasonably vivid, moderately clear and vivid, vague and dim **or** no image at all, you only "know" that you are thinking of the object.

Think of some relative or friend whom you frequently see (but who is not with you at present) and consider carefully the picture that comes before your mind's eye.

	' Perfectly clear and as vivid as normal vision'	**'Clear and reasonably vivid'**	**'Moderately clear and vivid'**	**'Vague and dim'**	**No image at all, you only "know" that you are thinking of the object**
1. The exact contour of face, head, shoulders and body					
2. Characteristic poses of head, attitudes of body, etc					
3. The precise carriage, length of step, etc., in walking					
4. The different colours worn in some familiar clothes					

Visualize a rising sun. Consider carefully the picture that comes before your mind's eye.

	'Perfectly clear and as vivid as normal vision'	**'Clear and reasonably vivid'**	**'Moderately clear and vivid'**	**'Vague and dim'**	**No image at all, you only " know" that you are thinking of the object**
5. The sun is rising above the horizon into a hazy sky.					
6. The sky clears and surrounds the sun with blueness					
7. Clouds. A storm blows up, with flashes of lightning					
8. A rainbow appears.					

Think of the front of a shop which you often go to. Consider the picture that comes before your mind's eye.

	'Perfectly clear and as vivid as normal vision'	**'Clear and reasonably vivid'**	**'Moderately clear and vivid'**	**'Vague and dim'**	**No image at all, you only "know" that you are thinking of the object**
9. The overall appearance of the shop from the opposite side of the road.					
10. **A** window display including colours, shapes and details of individual items for sale.					
11. You are near the entrance. The colour, shape and details of the door.					

12. You enter the shop and go to the counter. The counter assistant serves you. Money changes hands.					

Finally, think of a country scene which involves trees, mountains and a lake. Consider the picture that comes before your mind's eye.

	'Perfectly clear and as vivid as normal vision'	**'Clear and reasonably vivid'**	**'Moderately clear and vivid'**	**'Vague and dim'**	**No image at all, you only "know" that you are thinking of the object**
13. The contours **of** the landscape.					
14. The colour and shape of the trees.					
15. The colour and shape of the lake.					
16. A strong wind blows on the trees and on the lake causing waves.					

Appendix B: The Bucknell Auditory Imagery Scale - Vividness (BAIS-V)

For full details please see:

Halpern, A. R. (2015). Differences in auditory imagery self-report predict neural and behavioral outcomes. *Psychomusicology: Music, Mind, and Brain*, *25*(1), 37–47. https://doi.org/10.1037/pmu0000081

BAIS-V (vividness)

The following scale is designed to measure auditory imagery, or the way in which you "think about sounds in your head." For the following items you are asked to do the following: Read the item and consider whether you think of an image of the described sound in your head. Then rate the vividness of your image using the following "Vividness Rating Scale." If no image is generated, give a rating of 1.

Please feel free to use all of the levels in the scale when selecting your ratings.

Vividness Rating Scale

1	2	3	4	5	6	7
No image Present at All			Fairly Vivid			As Vivid As The Actual Sound

Vividness Rating

1. For the first item, consider the beginning of the song "Happy Birthday."
   The sound of a trumpet beginning the piece._____
2. For the next item, consider ordering something over the phone.
   The voice of an elderly clerk assisting you._____
3. For the next item, consider being at the beach.
   The sound of the waves crashing against nearby rocks. ______
4. For the next item, consider going to a dentist appointment.
   The loud sound of the dentist's drill.______
5. For the next item, consider being present at a jazz club.
   The sound of a saxophone solo.______
6. For the next item, consider being at a live baseball game.
   The cheer of the crowd as a player hits the ball._____

7. For the next item, consider attending a choir rehearsal.
   The sound of an all-children's choir singing the first verse of a song. ______

8. For the next item, consider attending an orchestral performance of Beethoven's Fifth.
   The sound of the ensemble playing. ______

9. For the next item, consider listening to a rain storm.
   The sound of gentle rain. ______

10. For the next item, consider attending classes.
    The slow-paced voice of your English teacher.______

11. For the next item, consider seeing a live opera performance.
    The voice of an opera singer in the middle of a verse.______

12. For the next item, consider attending a new tap-dance performance.
    The sound of tap-shoes on the stage.______

13. For the next item, consider a kindergarten class.
    The voice of the teacher reading a story to the children.______

14. For the next item, consider driving in a car.
    The sound of an upbeat rock song on the radio.______

Appendix C: The Bucknell Auditory Imagery Scale - Control (BAIS-C)

For full details please see:

Halpern, A. R. (2015). Differences in auditory imagery self-report predict neural and behavioral outcomes. *Psychomusicology: Music, Mind, and Brain*, *25*(1), 37–47. https://doi.org/10.1037/pmu0000081

The following scale is designed to measure auditory imagery, or the way in which you "think about sounds in your head." For the following pairs of items you are asked to do the following: Read the first item (marked "a") and consider whether you think of an image of the described sound in your head. Then read the second item (marked "b") and consider how easily you could change your image of the first sound to that of the second sound and hold this image. Rate how easily you could make this change using the "Ease of Change Rating Scale." If no images are generated, give a rating of 1. Please read "a" first and "b" second for each pair. It may be necessary to cover up "b" so that you focus first on "a" for each pair.

Please feel free to use all of the levels in the scale when selecting your ratings.

Ease of Change Rating Scale

1	2	3	4	5	6	7
No image present at all			Could Change the Image but with Effort			Extremely Easy to Change the Image

Change Rating

1. For the first pair, consider attending a choir rehearsal.
    a. The sound of an all-children's choir singing the first verse of a song.
    b. An all-adults' choir now sings the second verse of the song. ______

2. For the next pair, consider being present at a jazz club.
    a. The sound of a saxophone solo.
    b. The saxophone is now accompanied by a piano.______

3. For the next pair, consider listening to a rain storm.
    a. The sound of gentle rain.
    b. The gentle rain turns into a violent thunderstorm.______

4. For the next pair, consider driving in a car.
    a. The sound of an upbeat rock song on the radio.

   b. The song is now masked by the sound of the car coming to a screeching halt. ______

5. For the next pair, consider ordering something over the phone.
   a. The voice of an elderly clerk assisting you.
   b. The elderly clerk leaves and the voice of a younger clerk is now on the line.______

6. For the next pair, consider seeing a live opera performance.
   a. The voice of an opera singer in the middle of a verse.
   b. The opera singer now reaches the end of the piece and holds the final note. ______

7. For the next pair, consider going to a dentist appointment.
   a. The loud sound of the dentist's drill.
   b. The drill stops and you can now hear the soothing voice of the receptionist.______

8. For the next pair, consider the beginning of the song "Happy Birthday."
   a. The sound of a trumpet beginning the piece.
   b. The trumpet stops and a violin continues the piece.______

9. For the next pair, consider attending an orchestral performance of Beethoven's Fifth.
   a. The sound of the ensemble playing.
   b. The ensemble stops but the sound of a piano solo is present.______

10. For the next pair, consider attending a new tap-dance performance.
    a. The sound of tap-shoes on the stage.
    b. The sound of the shoes speeds up and gets louder.______

11. For the next pair, consider being at a live baseball game.
    a. The cheer of the crowd as a player hits the ball.
    b. Now the crowd boos as the fielder catches the ball._____

12. For the next pair, consider a kindergarten class.
    a. The voice of the teacher reading a story to the children.
    b. The teacher stops reading for a minute to talk to another teacher. ______

13. For the next pair, consider attending classes.
    a. The slow-paced voice of your English teacher.
    b. The pace of the teacher's voice gets faster at the end of class. ______

14. For the next pair, consider being at the beach.
    a. The sound of the waves crashing against nearby rocks.
    b. The waves are now drowned out by the loud sound of a boat's horn out at sea. _____

Appendix D: Pilot study for stimuli words for Chapter 3 TMS experiment

An online questionnaire was designed to determine what stimuli would be included in the Chapter 3 TMS experiment. Participants were asked to rate a word list for audio and visual features they associated with each word.

Method

Participants.

Undergraduate psychology students from the University of East Anglia (*N* = 43; 3 male) took part in return for course credit scheme (age range 18 – 29; *M* = 19.6; *SD* = 1.85). Participants signed up via the course credit participation system and were given a link to complete the questionnaire.

Stimuli & Procedure.

A total of 168 words were piloted. Participants were shown each word and to think about any visual and audio features they associated with the word. They were asked to rate on a scale of 1 (low) to 6 (high) how much they felt the word represented audio features, and the same for visual features.

Results

For each word a difference score was calculated by subtracting the average audio rating from the average visual rating. Words were categorised by the difference scores. Visual words were defined as scores between 1 and 4; multimodal words were defined as a difference score between 1 and -1; audio words were defined as -1 and -4. A total of 69 words were categorised as visual, 49 as audio, and 50 as multimodal.

The final stimuli set was combined with stimuli from Bonnici et al. (2016) to create the final set of 240 items, 80 items for each modality (audio; visual; multimodal). Audio items had an average rating of 4.94, and visual items an average rating of 4.97. The multimodal item average was 4.18, calculated by taking the averages of both the audio and visual ratings.

Appendix E: Object and Spatial Imagery Questionnaire (OSIQ)

For full details please see:

Blajenkova, O., Kozhevnikov, M., & Motes, M. A. (2006). Object-spatial imagery: A new self-report imagery questionnaire. *Applied Cognitive Psychology*, *20*(2), 239–263. https://doi.org/10.1002/acp.1182

One a scale of 1 to 5, please indicate how much you agree with the following statements.

1. I was very good in 3-D geometry as a student.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

2. If I were asked to choose between engineering professions and visual arts, I would prefer engineering.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

3. Architecture interests me more than painting.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

4. My images are very colourful and bright.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

5. I prefer schematic diagrams and sketches when reading a textbook instead of colourful and pictorial illustrations.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

6. My images are more like schematic representations of things and events rather than detailed pictures.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

7. When reading fiction, I usually form a clear and detailed mental picture of a scene or room that has been described.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

8. I have a photographic memory.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

9. I can easily imagine and mentally rotate 3-dimensional geometric figure.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

10. When entering a familiar store to get a specific item, I can easily picture the exact location of the target item, the shelf it stands on, how it is arranged and the surrounding articles.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

11. I normally do not experience many spontaneous vivid images; I use my mental imagery mostly when attempting to solve some problems like the ones in mathematics.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

12. My images are very vivid and photographic.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

13. I can easily sketch a blueprint for a building that I am familiar with.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

14. I am a good Tetris player.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

15. If I were asked to choose between studying architecture and visual arts, I would choose visual arts.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

16. My mental images of different objects very much resemble the size, shape and colour of actual objects that I have seen.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

17. When I imagine the face of a friend, I have a perfectly clear and bright image.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

18. I have excellent abilities in technical graphics.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

19. I can easily remember a great deal of visual details that someone else might never notice. For example, I would just automatically take some things in, like what colour is a shirt someone wears or what colour are his/her shoes.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

20. In high school, I had less difficulty with geometry than with art.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

21. I enjoy pictures with bright colours and unusual shapes like the ones in modern art.

1	**2**	**3**	**4**	**5**
Totally				**Totally**

disagree				**agree**

22. Sometimes my images are so vivid and persistent that it is difficult to ignore them.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

23. When thinking about an abstract concept (e.g. ‘a building’) I imagine an abstract schematic building in my mind or its blueprint rather than a specific concrete building.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

24. My images are more schematic than colourful and pictorial.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

25. I can close my eyes and easily picture a scene that I have experienced.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

26. I remember everything visually. I can recount what people wore to a dinner and I can talk about the way they sat and the way they looked probably in more detail than I could discuss what they said.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

27. I find it difficult to imagine how a 3-dimensional geometric figure would exactly look like when rotated.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

28. My visual images are in my head all the time. They are just right there.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

29. My graphic abilities would make a career in architecture relatively easy for me.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

30. When I hear a radio announcer or a DJ I’ve never actually seen, I usually find myself picturing what he or she might look like.

1	**2**	**3**	**4**	**5**
Totally disagree				**Totally agree**

Appendix F: Vividness of Object and Spatial Imagery (VOSI) Questionnaire

For full details please see:

Blazhenkova, O. (2016). Vividness of object and spatial imagery. *Perceptual and Motor Skills*, *122*(2), 490–508. https://doi.org/10.1177/0031512516639431

Try to imagine each of the items below to the best of your ability and then evaluate the vividness of your subjective mental imagery (pictures in your mind). For each of the items, please rate, on a scale from 1 to 5, the vividness of the evoked mental images. The scale is as follows:
5 = ‘Perfectly clear and vivid as normal vision’
4 = ‘Clear and reasonibaly vivd’
3 = ‘Moderately clear and vivid’
2 = ‘Vague and dim’
1 = ‘No image at all, you only “know” that you are thinking of the object’

		1	2	3	4	5
1.	Appearance of a candle fire					
2.	Colour mixing in an aquarelle painting of a floral bouquet					
3.	Play of colors of the sun reflecting on the water					
4.	Cutting-out and folding paper to create a 3D cube					
5.	Fine details and shape of a jellyfish					
6.	Rotation of 3D Tetris piece (3D shape) in order to fit a particular slot					
7.	Shape and color of an autumn leaf					
8.	Trajectory of an object moved by a force (e.g., in “angry birds” or billiard ball)					
9.	3D structure of a toilet flushing system					
10.	Shape of cloud in the sky					
11.	Mechanism of a mechanical wall clock					
12.	Fine details of zebra's skin					
13.	Schematical outline of a tractor from the 3 sides					
14.	Construction plan (three-dimensional schema) of a roller coaster					
15.	Location of your house on a map of your city					
16.	Pictorial details of the best friend's face					
17.	Plan of a multi-level road junction					
18.	Color pattern on a butterfly wing					
19.	Mechanism of a door handle					
20.	Splashes of colors in fireworks					
21.	Technical instruction for assembling a kitchen appliance (e.g., blender, food processor)					
22.	Play of colors in a bubble					

23.	Motion of the planets on a model of the solar system					
24.	Patterns on a peacock tail					
25.	Shapes and colors of a bonfire					
26.	Schema (plan) of a computer connection to a printer					
27.	Texture of your favorite clothes					
28.	Finding the way-out path in a paper maze					

Appendix G: Phenomenological rating questions for event memories in Chpater 4

While remembering the event, I feel as if I am reliving/experiencing it.

1	2	3	4	5	6	7
Not at all						As clearly as if it were happening right now

As I remember the event, I feel that I travel back to the time when it happened, that I am a participant in it again, rather than an outside observer tied to the present.

1	2	3	4	5	6	7
Not at all						As clearly as if it were happening right now

While remembering, it is as if I am experiencing the same feelings, emotions, and/or atmosphere again.

1	2	3	4	5	6	7
Not at all						As clearly as if it were happening right now

My memory for this event involves visual details.

1	2	3	4	5	6	7
Not at all						Completely

My memory for this event involves sounds.

1	2	3	4	5	6	7
Not at all						Completely

As I remember the event, it comes to me in words or in pictures as a coherent story or episode and not as an isolated face, observation, or scene.

1	2	3	4	5	6	7
Not at all						Definitely

As I remember, I experience a mental image of the event in my mind's eye.

1	2	3	4	5	6	7
Not at all						Perfectly clear and as vivid as normal vision

As I remember the event it comes to me in words.

1	2	3	4	5	6	7
Not at all						As much as any memory

While remembering, I experience a scene in which the elements of the setting are located relative to each other in space.

1	2	3	4	5	6	7
Not at all						Clear spatial layout

I believe the event occurred in the way I remember it and that I have not imagined or fabricated anything that did not occur.

1	2	3	4	5	6	7
100% imaginary						100% real

How positive or negative is this memory?

1	2	3	4	5	6	7
Very negative						Very positive

Since the event happened, I have thought and/or talked about this event.

1	2	3	4	5	6	7
Not at all						Many times

When you think about this memory, do you see it as if through your own eyes (1st person) or as an observer to the event (3rd person)?

Appendix H: Table of correlations for Chapter 4 – Experiment 2 with both unadjusted and adjusted values.

Table H.1. A table of each correlation comparison with unadjusted p-value and the adjusted value (also known as q-value) following Benjmaini-Hochberg adjustment to control for false discovery rate. Significant values following FDR value of 0.1 are marked with an asterix.

Comparison	**Unadjusted p-value**	**Adjusted value (q-value)**
Confidence (correct) & Spatial Imagery	.006	.066*
Confidence (incorrect) & Spatial Imagery	.015	.082*
Accuracy & Confidence (correct)	.022	.081*
Accuracy & Confidence (incorrect)	.075	.206
Accuracy & Spatial Imagery	.193	.425
Reaction Time & Spatial Imagery	.339	.622
Object Imagery & Spatial Imagery	.399	.627
Accuracy & Object Imagery	.660	.908
Reaction Time & Object Imagery	.702	.858
Confidence (correct) & Object Imagery	.797	.877
Confidence (incorrect) & Object Imagery	.968	.968