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**Behavioural and Neural Investigation of the
Subjective Experience of Remembering**

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This thesis is submitted for the degree of Doctor of Philosophy

September 2022

Declaration

This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in the preface and specified in the text. I further state that no substantial part of my thesis has already been submitted, or is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other university or similar institution except as declared in the preface and specified in the text. I hereby state that this thesis does not exceed the 60,000 word limit for the Faculty of Biology Degree Committee at the University of Cambridge.

The older adult raw structural MRI data and neuropsychological task data that I processed and analysed for the study presented in Chapter 3 is reported in the preprint by Helena M. Gellerson, Alexandra N. Trelle, Benjamin G. Farrar, Gillian Coughlan, Saana M. Korkki, Richard N. Henson, & Jon S. Simons. (2022). *Medial temporal lobe structure, mnemonic and perceptual discrimination in healthy older adults and those at risk for mild cognitive impairment*. bioRxiv. Retrieved from: <https://www.biorxiv.org/content/10.1101/2022.05.13.491810v2>.

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Abstract

The ability to recollect personal events in vivid multisensory detail from a first-person perspective is thought to be critical to the subjective experience of episodic memory. This PhD thesis comprises three experiments investigating these memory qualities and their parietal neural bases in different populations. The experiment presented in Chapter 2 used transcranial magnetic stimulation (TMS) in healthy younger adults and a novel associative memory task that manipulated stimulus modality to causally test whether the left angular gyrus (AnG) supports multimodal feature integration during episodic and semantic memory retrieval. Left AnG stimulation was found to selectively modulate response times in multimodal versus unimodal trials of both episodic associative recognition and semantic relatedness tasks, indicating AnG involvement in multiple forms of multimodal declarative memory retrieval. However, this stimulation effect was unexpectedly facilitatory rather than inhibitory, and no objective or subjective measures of episodic memory were modulated by AnG stimulation.

The experiment in Chapter 3 investigated the parietal neuroanatomical correlates of first-person versus third-person episodic recall in normal ageing using voxel-based morphometry and a custom 3D object location memory task that manipulated visual perspective during both encoding and retrieval. Compared to healthy younger adults, older adults showed a general deficit in first-person recall of object locations, irrespective of the original encoding perspective. Third-person recall was also impaired with age to a lesser extent and only when objects were encoded from the same third-person perspective. In older adults, left AnG and precuneus grey matter volume positively correlated with the adoption of a first-person recall perspective, but not first-person recall more generally. These parietal volumes were further shown to decline with age.

Finally, the experiment in Chapter 4 investigated whether individuals with self-reported mental imagery deficits (i.e., aphantasics) are impaired at first-person episodic recall. This was tested using a modified version of the task used in the previous chapter so that both object and spatial memory features, studied in first or third person, could be assessed via subjective vividness ratings and objective feature reproduction tasks. The visual perspective of spatial memory recall was additionally varied between the same and

alternative studied perspectives to test whether aphantasics are impaired at manipulating visuospatial representations. Despite globally lower vividness ratings relative to controls, aphantasics unexpectedly showed no deficits in object or spatial memory in either visual perspective. Together, these results further understanding of parietal contributions to memory and suggest investigation of those with atypical imagery as a promising line of future inquiry into the factors necessary for its subjective reliving.

Acknowledgements

First, I would like to express my deep gratitude to my PhD supervisor, Professor Jon Simons, for his guidance and support over the years. I would like to thank my funders, the Cambridge Trust and Queens' College, for my scholarship and continued assistance during the COVID-19 pandemic. I would also like to thank the research participants who took part in the experiments presented in this thesis.

I would like to give my thanks to all the members of the Cambridge Memory Lab for the many stimulating and thoughtful discussions. In particular, I would like to thank my office mate, Simon Kwon, for his assistance with TMS data collection for the study presented in Chapter 2. I would also like to give special thanks to Helena Gellersen and Saana Korkki for kindly sharing their unprocessed older adult structural MRI data and neuropsychological task data for use in the study presented in Chapter 3.

Finally, I am grateful to my parents, Liz and John, and my brother Zac, for their unwavering support and encouragement, particularly during the COVID-19 pandemic and the writing of this thesis.

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Chapter 1: General Introduction

An Introduction to Episodic Memory

Episodic memory is a form of long-term declarative (i.e., conscious) memory involving the ability to acquire, retain, and retrieve memories of specific personal events or “episodes” with a particular spatiotemporal context (Tulving, 2002). More broadly, episodic memory represents an expression of autonoetic consciousness (Tulving, 1985), an essential human attribute related to the sense of self and identity in subjective time. Thus, episodic remembering can be conceptualised as enabling a form of “mental time travel” into one’s personal past.

According to dual-process theories of episodic memory (Yonelinas, 1994; 2002; Yonelinas & Parks, 2007; Yonelinas et al., 2005; 2010), recognition of previously encountered events (e.g., situations from everyday life or, more commonly in the laboratory, experimental stimuli) can be supported by two distinct processes: *recollection* and *familiarity*. Under the dual-process view, recollection entails the remembering of specific contextual details associated with personal events and has been said to behave like a threshold process. By contrast, familiarity, which is characterised by the vague acontextual feeling of prior occurrence, is thought to reflect a signal detection-like assessment of a continuous memory strength signal. While the behavioural and neural separability of recollection and familiarity is not of direct relevance to this thesis (for reviews, see Rugg & Curran, 2007; Skinner & Fernandes, 2007; Yonelinas et al., 2010; see also Mandler, 2008; Wixted & Mickes, 2010; Wixted & Squire, 2010), it should be acknowledged that this debate has yet to be fully resolved, despite the popularity and influence of the dual-process view (for alternative perspectives, see DeCarlo, 2002; Donaldson, 1996; Dunn, 2004; Ingram, Mickes, & Wixted, 2012; Mickes, Wixted, & Wais, 2007; Wixted, 2007). Nevertheless, the phenomenological differences between recollection and familiarity provide a useful general framework in guiding thinking about the subjective experience of episodic remembering. Such distinctions between recollection and familiarity are perhaps best exemplified by Mandler’s famous hypothetical “butcher on the bus” scenario:

Consider seeing a man on a bus whom you are sure that you have seen before; you “know” him in that sense [familiarity]. Such a recognition is usually followed by a search process asking, in effect, Where could I know him from? Who is he? The search process generates likely contexts (Do I know him from work; is he a movie

star, a TV commentator, the milkman?). Eventually the search may end with the insight, That's the butcher from the supermarket [recollection]! (Mandler, 1980, pp. 252-253)

Various experimental paradigms have been employed to assess subjective (i.e., qualitative and experiential) and objective (i.e., quantitative and demonstrable) aspects of episodic memory retrieval. For instance, remember/know tasks probe the subjective level of awareness accompanying episodic memory retrieval by asking participants to categorise their experience of recalling studied memory items (e.g., pictures of objects or their spoken names) as “remembered” or “known”. “Remember” responses are given when specific contextual details of a memory are brought to mind, such as the “where” or “when” of a personal event, and thus reflect recollection. On the other hand, “know” responses are provided when memory items elicit only the vague acontextual sense of having been encountered before and therefore reflect familiarity. Other paradigms such as old/new recognition may instead task participants with the simple discrimination of several studied “old” and unstudied “new” memory items to measure episodic memory retrieval more objectively. In contrast to remember/know responses, however, old/new responses are considered to reflect the mixed contributions of recollection and familiarity, as recollection is often accompanied the feeling of familiarity (but not *vice versa*).

Although no test of recollection is likely to ever be truly process pure (Yonelinas et al., 2010), different aspects of recollection can be evaluated more directly. For example, recognition memory judgements can also be made on associations between two or more memory items, thus capturing a fundamental associative characteristic of recollection (i.e., personal events are typically comprised of multiple contemporaneous objects, people, or things). Recollection can also be examined via free recall and cued recall tasks, which provide different levels of retrieval support and thus reflect both the unconstrained spontaneity and controlled nature of recollection, depending on the circumstances. In comparison, source memory paradigms highlight the multidimensional quality of recollection, requiring participants to retrieve specific contextual features of individual episodes (i.e., the different external sensory/perceptual or internal mental details associated with a personal event). Additionally, autobiographical memory interviews (e.g., Kopelman, Wilson, & Baddeley, 1989; Levine et al., 2002) can be used to assess more naturalistic episodic memory concerning the details of personal life events experienced outside of the laboratory. Finally, a more complete impression of recollection can be gained by combining

such objective measures with subjective ones. For example, participants may be asked about the level of vividness (i.e., mental clarity or salience) with which they remembered a visual memory feature or their degree of confidence that that feature had been encountered before.

Episodic Memory in the Brain

Ever since the seminal report by Scoville & Milner (1957) of the patient H.M., who exhibited profound amnesia following bilateral medial temporal lobe resection, the medial temporal lobes have been regarded as crucial for episodic memory. The medial temporal lobes can be divided into the hippocampus (HPC) and its subfields as well as the perirhinal, entorhinal, and parahippocampal cortices. Regarding recollection and familiarity, there does not appear to be a direct functional mapping onto these medial temporal subregions (Diana, Yonelinas, & Ranganath, 2007; Squire, Stark, & Clark, 2004), or even within them (e.g., Merkow, Burke, & Kahana, 2015; Smith, Wixted, & Squire, 2011; Wais, Squire, & Wixted, 2010; Wixted & Squire, 2010). However, the HPC is widely held to be particularly important for episodic memory (Eichenbaum, Yonelinas, & Ranganath, 2007; Moscovitch et al., 2016; O'Keefe & Nadel, 1978; Squire & Zola-Morgan, 1991; Tulving & Markowitsch, 1998). More specifically, the HPC is thought to support several processes necessary for the initial formation (i.e., encoding), long-term retention, and retrieval of episodic memories (Eichenbaum, 2000). These HPC-supported mnemonic processes include *pattern separation*, *systems consolidation*, and *pattern completion*.

Pattern separation is the process whereby representations of everyday experiences, which typically overlap in their features, are made more distinctive. This process begins during encoding in the dentate gyrus, which orthogonalizes incoming sensory input patterns into non-overlapping output patterns via sparse coding (i.e., individual memories are coded by a small subset of neurons and each neuron codes a few memories) (Norman & O'Reilly, 2003; McClelland, McNaughton, & O'Reilly, 1995; Rolls, 2013; 2016). These memory traces initially depend on both the HPC and wider neocortex, which represents disparate sensory event features, but get reorganised with the aid of the HPC, to eventually become independent of the HPC through the process of systems consolidation (Squire et al., 2015; but see Nadel et al., 2007). Evidence for HPC-mediated systems consolidation can be found in patients with medial temporal lobe damage like H.M., who show greater amnesia for recent compared to remote memories (Squire, 2009). In contrast to pattern separation, pattern completion entails the cortical reinstatement (i.e., reactivation of encoding-related activity patterns during episodic memory retrieval) of a complete memory trace from a partial

retrieval cue. The auto-associative nature of pattern completion (e.g., recalling a person's name from a face retrieval cue, or *vice versa*) has been linked to dense recurrent collateral connectivity within the CA3 hippocampal subfield, which acts as a single attractor network enabling rapid associations to be formed between arbitrary neocortical ensembles representing whole memories (Norman & O'Reilly, 2003; McClelland, McNaughton, & O'Reilly, 1995; Rolls, 2013; 2016). Accordingly, the degree of cortical reinstatement has been observed to correlate with HPC activity (Horner et al., 2015; Staresina et al., 2012). In summary, the HPC supports a variety of important processes that minimise interference between similar stored event memories (pattern separation), stabilise those memories with time (systems consolidation), and facilitate holistic recollection from fragmentary inputs (pattern completion).

Damage to the frontal lobes has also been shown to impair certain aspects of episodic memory. For example, patients with frontal lobe lesions can recall memory items but show deficits in recollecting their study context (i.e., source) (Janowsky, Shimamura, & Squire, 1989) or temporal order (Shimamura, Janowsky, & Squire, 1990). Relatedly, patients with the frontal variant of frontotemporal dementia perform at floor level on source discrimination tasks (Simons et al., 2002), suggesting contextual recollection is particularly affected by frontal lobe damage. However, patients with surgical frontal lobe excisions can perform normally when strategies are supplied during encoding and retrieval, despite impaired free recall, and the introduction and removal of interfering cues modulates cued recall performance (Incisa della Rochetta & Milner, 1993). Thus, in line with its well-established role in cognitive control (Miller, 2000), the prefrontal cortex (PFC) of the frontal lobes is thought to interact with other key memory regions such as the medial temporal lobes to support mnemonic control processes (Eichenbaum, 2017; Simons & Spiers, 2003). Generally, these PFC-mediated control processes, in conjunction with those supported by medial temporal lobe structures, can be deployed during encoding as well as retrieval to optimise episodic memory (for review, see Blumenfeld & Ranganath, 2007). For instance, the PFC can promote effective encoding by supporting organisational (Blumenfeld & Ranganath, 2006) or elaborative strategies (Davachi, Mitchell, & Wanger, 2003). During retrieval, the PFC may also help resolve interference between competing response tendencies (Peters et al., 2013).

Functional neuroimaging has demonstrated several anatomical and functional subdivisions within the PFC, with each facilitating different aspects of cognitive control over memory. First, functional magnetic resonance imaging (fMRI) activity in the PFC seems to

be lateralised according to material type. For example, recognition of verbally encoded (i.e., acquired) materials activates the left dorsolateral PFC whereas nonverbal materials activate the right dorsolateral PFC (Opitz, Mecklinger, Friederici, 2000). Such lateralisation of activity can even be observed across different nonverbal stimulus categories, such as faces and objects (Simons et al., 2001). Second, other distinctions can be found between the lateral and medial surfaces of the PFC in terms of processing reward- or self-related information and exerting top-down cognitive control in line with retrieval goals (Eichenbaum, 2017; Elliott, Dolan, & Frith, 2000; Euston, Gruber, & McNaughton, 2012; Maguire, Vargha-Khadem, & Mishkin, 2001). Finally, lateral PFC function can be further divided by ventral and dorsal regions, with the former supporting retrieval cue specification and maintenance processes and the latter supporting the monitoring and manipulation of retrieved information (Dobbins et al., 2002; Henson, Shallice, & Dolan, 1999). During encoding, the ventrolateral PFC supports the selection of goal-relevant item information whereas the dorsolateral PFC plays a role in organising those items in working memory to promote long-term memory formation (Blumenfeld & Ranganath, 2007). It should be cautioned, however, that such findings do not necessarily indicate sharp functional parcellation of subregions. Indeed, other work has called this view into question, instead arguing for graded subregional functional specialisation based on graded transitions in network connectivity within the PFC (Jackson et al., 2020; Jung, Lambon Ralph, & Jackson, 2022). Likewise, evidence for graded intra-region network connectivity has been found within the temporal lobes (Binney, Parker, & Lambon Ralph, 2012; Bajada et al., 2017) and parietal cortex (Daselaar et al., 2013; Humphreys, Jackson, & Lambon Ralph, 2020; Humphreys & Tibon, 2022), implying a potentially wider organising principle of higher order association cortices (Jung et al., 2017).

Of particular relevance to this thesis, functional neuroimaging reviews have also frequently highlighted lateral ventral parietal cortex (VPC) functional magnetic resonance imaging (fMRI) activation, specifically within the left angular gyrus (AnG) (see Figure 1 A for anatomical location), during episodic memory retrieval (Rugg & King, 2018; Rugg & Vilberg, 2013; Sestieri, Shulman, & Corbetta, 2017; Wagner et al., 2005). This part of the VPC belongs to an ensemble of brain regions referred to as the *core recollection network* (Hayama, Vilberg, & Rugg, 2012; Johnson & Rugg, 2007), which additionally comprises the PFC, medial temporal structures including the HPC and parahippocampal cortex as well as more posterior retrosplenial and posterior cingulate cortices (see Figure 1 B). These core recollection regions collectively show greater levels of fMRI activation during successful

versus failed recollection across a variety of experimental procedures and materials (Kim, 2010; Rugg & Vilberg, 2013; Thakral, Wang, & Rugg, 2017). Compared to the recollection sensitive VPC, more dorsal parietal regions such as the intraparietal sulcus are associated more with the non-specific sense of familiarity (for reviews, see Hutchinson et al., 2009; Wagner et al., 2005). The neuroimaging findings regarding the posterior VPC are in striking contrast to the early neuropsychological evidence, where parietal brain damage seemingly did not produce serious memory impairments on many standard memory assessments (Berryhill et al., 2007; Davidson et al., 2008; Haramati et al., 2008; Simons et al., 2008). These patient observations, combined with the aforementioned neuroimaging evidence, have been the subject of much controversy (e.g., Simons & Mayes, 2008) and have inspired numerous hypotheses regarding the possible mnemonic function(s) of the parietal lobes. An overview of these theoretical accounts is provided in the next section.

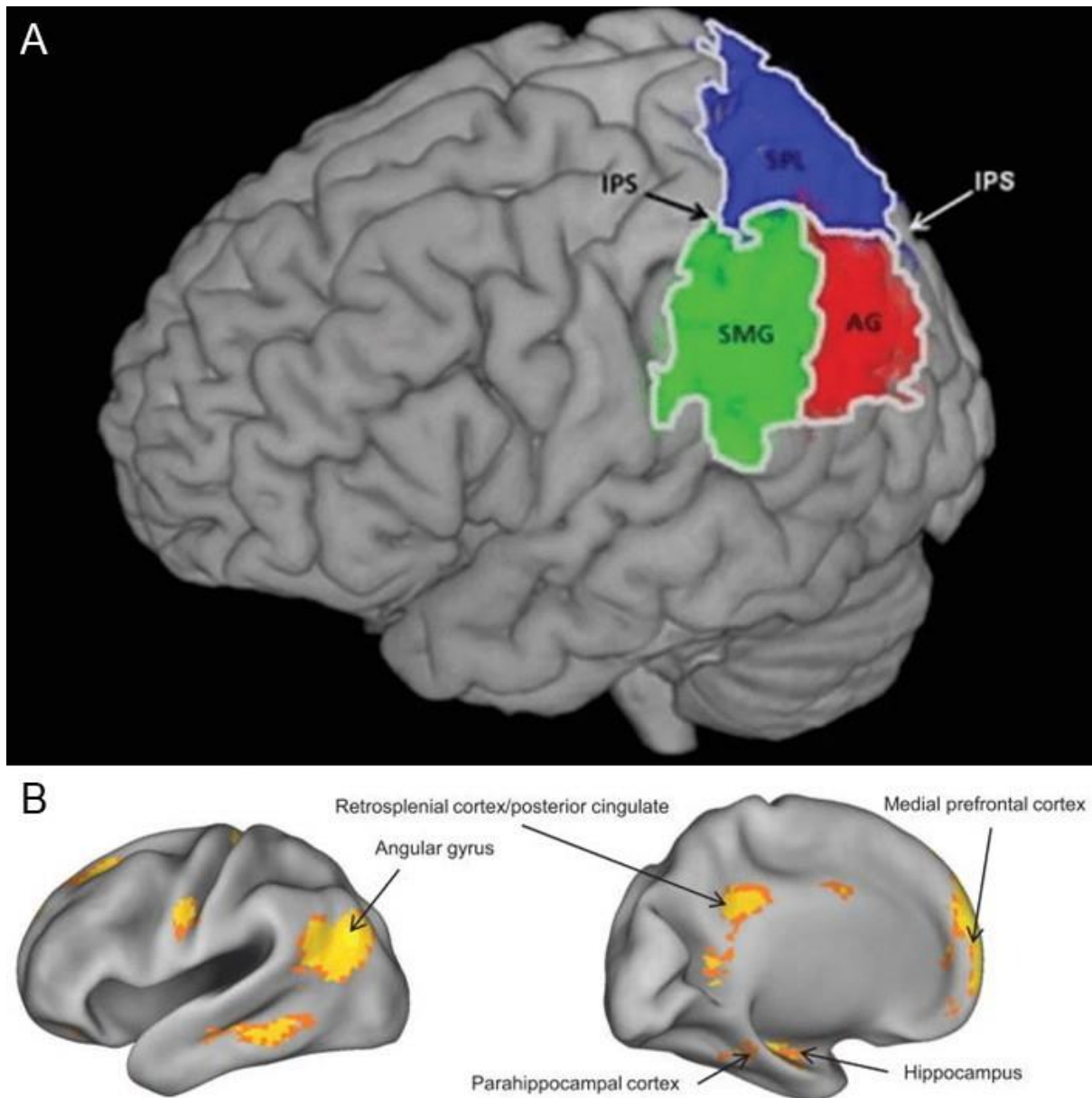


Figure 1. A) Gross anatomical subdivisions of the lateral posterior parietal cortex taken from Humphreys & Tibon (2022). The superior parietal lobule, situated in the dorsal posterior parietal cortex, is shaded in blue. Supramarginal and angular gyri, respectively shaded in green and red, comprise the ventral posterior parietal cortex. Dorsal and ventral posterior parietal regions are demarcated by the intraparietal sulcus. B) Example fMRI activation map taken from Rugg & Vilberg (2013) to illustrate the core recollection network. Shaded areas denote brain regions associated with a greater neural response to correctly recognised test words endorsed as “remembered” (i.e., successfully recollected) than “known” (i.e., recognised on the basis of familiarity), regardless of whether the test words were studied as pictures or words.

Parietal Lobe Involvement in Episodic Memory

In their influential neuroimaging review, Wagner et al. (2005) considered three possible hypotheses regarding the role of the lateral posterior parietal cortex (PPC) in

episodic memory retrieval: the *mnemonic accumulator hypothesis*, the *attention to internal representations hypothesis*, and the *output buffer hypothesis*. To briefly summarise, the mnemonic accumulator hypothesis proposes that the PPC temporally integrates information until a decision criterion is reached to endorse items as “old”. The attention to internal representations hypothesis instead posits that the PPC directs attention to internal mnemonic representations. By contrast, the output buffer hypothesis holds that the PC supports mnemonic decision making by temporarily holding the contents of retrieval in working memory, akin to Baddeley’s (2000) working memory “episodic buffer”. Although several other accounts have been advanced since, most fall broadly under one or some combination of these three hypotheses, which I will classify more generally as decisional, attentional, and content accounts.

Decisional accounts (e.g., Wagner et al., 2005) have received the least scrutiny, and rest largely on the finding that lateral parietal cortex activity tracks the perceived oldness of memory items, irrespective of study status (Wheeler & Buckner, 2004; Kahn, Davachi, & Wagner, 2004). Furthermore, dorsal PPC regions such as the intraparietal sulcus have also been linked to supporting perceptual decision making (Gold & Shadlen, 2007). Such observations have led to the proposal that the intraparietal sulcus supports a domain-general evidence accumulation mechanism underpinning both episodic memory and perceptual recognition judgements (Ploran et al., 2007). As noted by Berryhill (2012), however, disrupted parietal function does not result in the general memory deficit that would be expected from gauging a dysfunctional memory strength index (Berryhill, Drowos, & Olson, 2009; Drowos et al., 2010; Haramati et al., 2008; Yazar, Bergström, & Simons, 2014), and this perspective has received comparatively less interest than attentional and content accounts.

Although the attention to internal representations hypothesis (Wagner et al., 2005) made no functional distinctions between different PPC regions, later proposals have. For example, the *dual attentional processes* account (Cabeza, 2008) argued that dorsal PPC serves top-down allocation of attention according to retrieval goals whereas ventral PPC supports bottom-up capture of attention by recollected event details. This model was later extended in the *attention to memory* account (Cabeza et al., 2008; Cabeza, Ciaramelli, & Moscovitch, 2012; Ciaramelli, Grady, & Moscovitch, 2008; Ciaramelli & Moscovitch, 2020; Olson & Berryhill, 2009) to explain dorsal PPC involvement during different stages of episodic memory retrieval. Under this view, dorsal PPC operates both before retrieval, to

allocate top-down attention to maintain goal states and relevant retrieval cues, and after retrieval, to support retrieval monitoring and evaluation when making mnemonic decisions.

Dual attentional accounts broadly agree with theories of frontoparietal networks supporting different aspects of visuospatial attention (Corbetta & Shulman, 2002; Corbetta, Patel, & Shulman, 2008; Wolfe & Horowitz, 2017) as well as with some of the parietal patient evidence *vis-à-vis* memory. For example, Berryhill et al. (2007) showed that patients with bilateral lobe lesions perform normally when their autobiographical memories are cued, but not when they are freely recalled, which is considered to depend largely on the spontaneous capture of attention by such memories. Moreover, Ciaramelli et al. (2010a) compared patients with dorsal and ventral parietal lesions and found that those with ventral lesions were relatively slower to respond to invalidly cued targets, which are similarly thought to capture bottom-up attentional processes. Dorsal/ventral distinctions in PPC attentional function during episodic memory retrieval have also been suggested to mirror those during episodic memory encoding (for review, see Uncapher & Wagner, 2009), where encoding-related activity in the dorsal and ventral PPC is associated with the subsequent success and failure of episodic recall, respectively (Uncapher, Hutchinson, & Wagner, 2011).

While more anterior regions of the VPC, namely the supramarginal gyrus and temporoparietal junction, appear to serve the reflexive attentional processes classically ascribed to the wider VPC (Cabeza et al., 2011; Hutchinson, Uncapher, & Wagner, 2009; Hutchinson et al., 2014), the posterior part, the AnG, presents a challenge to overarching attentional accounts. In a recent fMRI study, Ciaramelli et al. (2020) manipulated study repetitions and retrieval goals in a recognition memory task to test the dual-process attentional account. They reasoned that since study repetitions should lead to more salient memories, bottom-up attentional capture during recognition of repeatedly studied items should lead to increased activity in the VPC versus items only studied once. While the supramarginal gyrus showed this activation profile, the AnG showed the opposite, suggesting an anterior/posterior subdivision within the VPC. Furthermore, disrupting VPC function does not seem to affect performance in many studies where memory tasks involved direct attentional manipulations. For example, Simons et al. (2010) showed that reducing the behavioural relevance of mnemonic information critical to source recollection did not affect performance in bilateral parietal lesion patients. Non-invasive brain stimulation techniques, which can temporarily intervene in neural processing within targeted regions to establish their causal role in behaviour, have brought further clarity on this issue. For instance, Yazar,

Bergström, & Simons (2014) found in healthy younger adults that free recall was no more impaired than cued recall of words following continuous theta burst stimulation targeting the left AnG, contrary to what would be expected of disrupted bottom-up attentional processes. In a later brain stimulation study using the same protocol, Bonnici et al. (2018) showed that left AnG stimulation selectively reduces free recall of ABMs, replicating Berryhill et al.'s (2007) findings, but not word pairs. As both forms of free recall are assumed to spontaneously capture attention, these results reinforce the notion that this region of the VPCs supports non-attentional processes. Indeed, the VPC is now widely accepted to be a functionally heterogeneous region, with respective anterior/posterior subdivisions in bottom-up attentional and episodic functions (Ciaramelli et al., 2020; Hutchinson, Uncapher, & Wagner, 2009; Hutchinson et al., 2014; Sestieri, Shulman, & Corbetta, 2017).

Another challenge to overarching attentional accounts for VPC mnemonic function comes from findings indicating the region's involvement in mnemonic representation. For example, VPC activity has often been shown to covary with the amount of retrieved information in functional neuroimaging studies (Guerin & Miller, 2011; Hayama, Vilberg, & Rugg, 2012; Vilberg, Moosavi, & Rugg, 2006; Vilberg & Rugg, 2007; 2008; 2009a; 2009b; Yu, Johnson, & Rugg, 2012). Similarly, left parietal old/new event-related potential effects have been shown to index the quality and volume of contextual information during retrieval (Doidge et al., 2017) and AnG fMRI activity tracks the fidelity with which episodic memories are recollected (Richter et al., 2016). More recently, multivoxel pattern analysis has been employed to decode the content of retrieval within the vicinity of the AnG (Bird et al., 2015; Bonnici et al., 2016; Kuhl, Johnson, & Chun, 2013; Kuhl & Chun, 2014; Lee & Kuhl, 2016; Rissman et al., 2016; St-Laruent, Abdi, & Buchsbaum, 2015; Thakral, Wang, & Rugg, 2017). An alternative explanation for this latter set of findings, which are often category-specific, is that such activity patterns might simply reflect the differential engagement of category-specific cognitive processes rather than retrieved memory representations (Davis & Poldrack, 2013). However, the decoding of individual multimodal episodic memories from left AnG activity patterns (Bonnici et al., 2016) makes this perspective less likely. However, it should be acknowledged that, whereas posterior ventral PPC may represent retrieved episodic features independent of current retrieval goals (Guerin & Miller, 2011), dorsal PPC may do so according to specific retrieval goals (Favila et al., 2018), paralleling in some respects the functional divisions proposed in dual attentional accounts.

One question arising from the above findings is whether VPC regions such as the AnG support long-term stored mnemonic representations or instead temporarily buffer retrieved memory contents. According to the *cortical binding of relational activity* (CoBRA) account (Shimamura, 2011), the VPC functions as a convergence zone for multimodal episodes, where distinct episodic features represented by disparate cortical regions are bound and eventually stored during the final stages of memory consolidation. Supporting this view, the AnG is well situated in the brain at a nexus between various sensory association cortices, showing reciprocal white matter and strong resting-state connectivity with modality-specific sensory association cortices (Seghier, 2013; Uddin et al., 2010). Moreover, functional neuroimaging and causal brain stimulation evidence attest to the preferential retrieval processing of multimodal episodes by the left AnG. In an fMRI study, Bonnici et al. (2016) found greater fMRI activity in the left AnG during the retrieval of multimodal audio-visual clips than unimodal audio or visual clips. Multivoxel pattern analysis further revealed that individual multimodal episodes could be decoded from activity patterns within the same region. Lending further support, Yazar, Bergström, & Simons (2017) demonstrated that inhibitory continuous theta burst stimulation of the left AnG disrupts the episodic retrieval of multimodal concurrent object-in-scene and spoken object name stimuli, but not either feature separately. Inconsistent with CoBRA theory, however, these multimodal retrieval effects are observed in the left AnG soon after encoding, presumably before any significant degree of memory consolidation could occur (but see Tibon et al., 2019). Consistent with information buffering accounts (Humphreys & Lambon Ralph, 2015; Guerin & Miller, 2011; Rugg & King, 2018; Vilberg & Rugg, 2008; Wagner et al., 2005), however, VPC activity scales with the duration of stimulus presentation (Vilberg & Rugg, 2009a) and tracks the period over which recollected information is maintained (Vilberg & Rugg, 2012; 2014). Thus, the current evidence supports the view that the left AnG plays a role in the online representation of multimodal episodes, rather than the reactivation of integrated long-term stored representations as suggested by CoBRA theory.

Functional neuroimaging indicates semantic and episodic memory may recruit overlapping networks of brain regions including the AnG (Binder et al., 2009; Binder & Desai, 2011; Kim, 2016; Rajah & McIntosh, 2005). Such findings raise the possibility that different forms of declarative memory may in some cases be supported by the same processes, mediated by the same brain regions. On this basis, some have proposed a central role for the AnG in semantic processing, placing the region “at the top of a processing

hierarchy underlying concept retrieval and conceptual integration” (Binder et al., 2009, p. 2776), although this perspective is difficult to reconcile with evidence establishing the bilateral anterior temporal lobes as a critical amodal semantic hub (for review, see Lambon Ralph, 2013). Binder & Desai (2011) later argued that the activity of a common declarative memory network may reflect the retrieval of conceptual knowledge, which may serve as a fundamental building block for mental scene construction during recollection. Under this view, the AnG has been proposed to support even concepts “in which entities interact in space and time” (Binder & Desai, 2011, p. 530) based on its importance to spatial cognition and that of nearby parietal and posterior temporal regions to action and movement perception (Kravitz et al., 2011). Others such as Seghier (2013) have instead proposed that the AnG might serve as a domain-general crossmodal integrative hub where multimodal inputs converge for integration and give rise to a variety of representations, depending on the task. In their fMRI study, Bonnici et al. (2016) additionally examined the retrieval of words associated with unimodal and multimodal features in a semantic relatedness task to test whether the region plays a role in multimodal semantic integration. However, the results were ambiguous as unlike multimodal episodic memory retrieval, unimodal and multimodal semantic retrieval engaged the AnG to an equivalent degree, which might simply reflect the potentially inherently multimodal or amodal nature of semantic memory representations.

It should be noted that the AnG is not universally accepted to be an important region for semantic memory retrieval. Contrary its response profile during episodic tasks, the AnG often shows deactivation during semantic tasks relative to rest (Humphreys et al., 2021; 2022; Humphreys & Lambon Ralph, 2017; Humphreys, Jung, & Lambon Ralph, 2022; King & Rugg, 2018). Furthermore, the extent of AnG deactivation during semantic memory retrieval may be related to domain-general task difficulty rather than semantic processing (Humphreys & Lambon Ralph, 2017; Humphreys, Jung, & Lambon Ralph, 2022). Indeed, semantic contrasts typically compare easy versus hard conditions (e.g., words versus pseudowords or concrete versus abstract words). However, other work combining multiple fMRI studies has identified separable effects of domain-general task difficulty and domain-specific semantic processing demand within the bilateral AnG, with stronger difficulty effects in anterior than posterior subregions and stronger semantic effects in left than right hemispheres (Kuhnke et al., 2023). Additionally, the AnG showed an inconsistent response polarity across these studies when rest was used as a baseline condition, but consistent relative differential activity between semantic and non-semantic task conditions. Based on this evidence, the authors

argued that rest may not be an appropriate baseline condition when investigating semantic processing as rest is not process-neutral (Stark & Squire, 2001; Morcom & Fletcher, 2007) and may also involve some degree of semantic processing. Nevertheless, task difficulty effects are an important potential confound to consider when evaluating evidence for AnG involvement in semantic functions.

More recent unifying proposals such as the *parietal unified connectivity-biased computation* (PUCC) model (Humphreys & Lambon Ralph, 2015) have instead focused on temporary online multimodal information buffering of spatiotemporally extended representations as a key and shared AnG-mediated function underpinning the conscious and dynamic reflection on one's episodic and semantic memories (Humphreys, Lambon Ralph, & Simons, 2021). This core process of information buffering may be shared across the wider lateral parietal cortex, where regional/subregional differences in connectivity shape its expression (Humphreys & Tibon, 2022). Supporting the notion of more domain-general information buffering within the AnG, non-episodic tasks involving the “temporal unfolding of information” like the integration of semantic information during the reading of narratives have been shown to activate the AnG (Branzi et al., 2020). Online TMS of the same region during narrative reading has also recently been demonstrated to disrupt online context-dependent integration (Branzi et al., 2021).

As noted by Humphreys & Tibon (2022), the PUCC model may account for a wider range of observations than other models. For example, a temporo-spatial information buffer may serve episodic processing more generally, aiding both the recollection of previous events and simulation of future ones (Thakral, Madore, & Schacter, 2017). Due to reduced connectivity with the prefrontal cognitive control regions, the engagement of more automatic information buffering in the ventral parietal cortex specifically may also explain dorsal/ventral functional distinctions attributed to attentional processes by others (e.g., Cabeza, Ciaramelli, & Moscovitch, 2012). Long-term statistical learning may also result from repeated information buffering (Humphrey, Lambon Ralph, & Simons, 2021), giving rise to the formation of generalisable mental frameworks/associative knowledge structures (i.e., schemas), an aspect of cognition also attributed to the AnG (Wagner et al., 2015). Indeed, AnG involvement has been suggested in myriad functions beyond episodic and semantic memory retrieval. These include visuospatial attention, body awareness and motor planning, number processing, word reading and comprehension, social cognition, and spatial cognition (for reviews, see Seghier, 2013; 2023; Wagner & Rusconi, 2023), although it should be noted

that much previous work has mixed AnG with neighbouring regions (Seghier, 2013). Thus, the PUCC model may help resolve apparent inconsistencies between more domain-specific accounts of AnG function (and possibly that of wider lateral parietal cortex) by providing a fundamental information buffering mechanism that, depending on local variations in network connectivity, may support an array of cognitive activities.

The Subjective Experience of Remembering

While parietal lesion patients can indeed exhibit intact episodic retrieval, particularly when recall is cued (Berryhill et al., 2007; Simons et al., 2008; but see Ben-Zvi, Soroker, & Levy, 2015), their memory is not entirely normal. For example, Davidson et al. (2008) and Drowos et al. (2010) showed that despite largely intact performance on a variety of episodic memory tasks, parietal-damaged patients make less frequent recollection-based “remember” responses than age-matched neurologically healthy controls in remember/know tasks that probe the subjective experience of episodic retrieval. Simons et al. (2008; 2010) additionally demonstrated that such patients also report less confidence in their memory and diminished vividness of recollection, despite normal source memory accuracy. Finally, Hower et al. (2014) used a receiver-operating characteristic analysis to show that old/new recognition decision criteria for unstudied new items is unaffected by bilateral parietal lesions, but the willingness to endorse studied old items with high confidence is reduced. Consistent with prior findings, these patients did not show impairments in recognition accuracy either.

Similar patterns of performance to the parietal-damaged patients have been replicated in healthy younger adults using non-invasive brain stimulation. As noted previously, Yazar, Bergström, & Simons (2014) found no effect of inhibitory AnG stimulation on free recall of word pairs. Participants in this study further showed no deficits in objective memory performance more generally as assessed by a battery of old-new recognition, cued recall, and source recollection tasks. However, a selective left AnG stimulation effect was found on confidence in source memory and no other task. Relatedly, inhibitory AnG stimulation has been found to alter response bias in source memory tasks (i.e., the tendency to provide a given source response regardless of the ability to accurately discriminate the source) (Sestieri et al., 2013) as well as the perceived difficulty of episodic, but not non-episodic, tasks (Bonnici et al., 2018; Thakral, Madore, & Schacter, 2017). Functional neuroimaging also indicates regions of the PPC to be sensitive to the qualitative richness of episodic memories. For instance, Richter et al. (2016) used a continuous memory paradigm allowing the behavioural and neural separation of the overall success and precision of episodic memory

retrieval, and showed that fMRI activity in the left AnG tracks the fidelity with which visual scenes are remembered, whereas HPC activity was associated with whether those scenes were remembered overall.

First based on the apparent disagreement between objective and subjective aspects of episodic memory in parietal lesion patients, the *subjective experience of remembering* hypothesis (Ally et al., 2008; Simons, 2008; see also Davidson et al., 2008; Moscovitch et al., 2016) posits that the VPC supports processes enabling the subjective reliving of past experiences. Later formulations of the subjective memory account (Yazar, Bergström, & Simons, 2012; 2014; 2017; for current review, see Simons, Fernyhough, & Ritchey, 2022) have proposed the left AnG to support vivid reminiscence by integrating multisensory features within an egocentric (i.e., self-referential) framework during retrieval. As noted by Moscovitch et al. (2016), the absence of objective source memory effects in much of the patient evidence may simply reflect the fact that such tasks do not typically encourage multimodal episodic retrieval, instead probing specific aspects of recollection. Indeed, as outlined previously, functional neuroimaging (e.g., Bonnici et al., 2016) and causal brain stimulation (e.g., Yazar, Bergström, & Simons, 2017) work, which directly manipulated stimulus modality, has since accrued good evidence for the preferential processing by the left AnG of multimodal episodes during retrieval.

The second part of the subjective experience of remembering hypothesis—that AnG-supported episodic retrieval processes operate within an egocentric framework—was initially motivated by findings indicating the PPC supports egocentric aspects of cognition (e.g., Stein, 1992). One example is hemispatial neglect, a disorder of egocentric spatial awareness that is classically associated with lesions to the PPC (Driver & Mattingley, 1998; Karnath & Rorden, 2012). Furthermore, the AnG is a member of the *default mode network* (Buckner, Andrews-Hanna, & Schacter, 2008), the activity of which is generally associated with self-referential mental activities such as daydreaming and thinking about the personal past or future. With respect to memory more specifically, Ciaramelli et al. (2010b) found evidence suggesting that PPC damage impairs route navigation in remote spatial memory tasks. Route navigation is thought to depend on an egocentric spatial reference frame due to the emphasis it places on the relationship between one's body and the environment (e.g., sequencing landmarks along a route). This can be contrasted against map-like and viewpoint-independent allocentric reference frames, which are instead associated with specific cell types in medial temporal lobe structures such as the HPC and entorhinal cortex (Ekstrom et al., 2003; Epstein

et al., 2017; Hafting et al., 2005; O’Keefe & Nadel, 1978). Most critically, Ciaramelli et al. (2010b) additionally found that PPC lesion patients reported weaker re-experiencing during navigation, which additionally lacked a first-person (i.e., own-eyes) perspective.

An own-eyes *first-person* visual perspective fundamentally differs from an observer-like *third-person* perspective in terms of its endogenous origin. As such, a first-person visual perspective is inherently egocentric. In the context of episodic memory retrieval, a first-person relative to a third-person visual perspective has consistently been behaviourally associated more with the sensory/perceptual and internal details of personal events, which comprise the feelings, sensations, and thoughts associated with those events (Berntsen & Rubin, 2006; McIsaac & Eich, 2002; Robinson & Swanson, 1993; Sutin & Robins, 2010). Such a constellation of features attest to richness and variety of subjective recollective experience. Indeed, subjective ratings of memory vividness have been shown to correlate with autobiographical memory recall from a first-person perspective (e.g., Rice & Rubin, 2011).

As with egocentric spatial memory, investigation into the neural bases of first-person perspective episodic remembering has implicated the involvement of different PPC regions. For example, activity in the precuneus, a region located on the medial surface of the dorsal PPC, has been linked to memory-related *mental imagery* (i.e., internal sensory experience of some object, person, event, or scene in their physical absence) (Fletcher et al., 1995; Cavanna & Trimble, 2006), and its volume has been positively correlated with first-person perspective autobiographical memory recall (Freton et al., 2014; Hebscher, Levine, & Gilboa, 2018). Furthermore, activity in both the precuneus and AnG has been tied to shifting from a first-person own-eyes perspective to a third-person observer perspective during episodic recall across several studies (Iriye & St. Jacques, 2018; Marcotti & St. Jacques, 2018; St. Jacques, Szpunar, & Schacter, 2017). Similarly, Russell et al. (2019) showed that patients with right hemisphere parietal damage have deficits in judging whether 3D real world scenes were previously viewed from their own or an observer’s perspective, despite exhibiting unimpaired item and location memory. In the same study, but in a separate group of neurologically healthy participants, Russell et al. used multi-voxel pattern analysis to further show that patterns of activity around the AnG are sensitive to such perspective shift judgements. Finally, Bonnici et al. (2018) showed that continuous theta burst stimulation of the left AnG decreases the likelihood of recalling autobiographical memories from a first-person perspective. Such findings have led to the proposal that a first-person visual perspective may

be an essential factor underlying subjective memory reliving (Simons, Ritchey, & Fernyhough, 2022; Zaman & Russell, 2022). However, while links between egocentric memory retrieval and dorsal and ventral PPC have been established, the precise contributions of these regions have remained elusive.

Thesis Overview

This thesis aimed to further develop the subjective memory hypothesis, with a focus on the processes supported by the PPC that give rise to the feeling of episodic memory reliving. To this end, I devised multiple custom experimental paradigms and used different techniques to test different aspects of this hypothesis in different populations. In my first experimental chapter, I will present a non-invasive brain stimulation study in which I causally tested a potentially unifying account for AnG mnemonic function, that the region supports a mechanism of multimodal feature integration common to episodic and semantic memory retrieval. In my second experimental chapter, I will present a voxel-based morphometry study that intended to help disentangle potential differences in the contribution of different PPC regions to first-person episodic memory retrieval during normal ageing. Finally, in my third experimental chapter, I will present an online behavioural study in which I explored potential differences in the visual perspective and vividness of episodic memory in individuals with weak mental imagery, a non-clinical condition referred to as “aphantasia” (see Zeman et al., 2015).

Chapter 2: The Angular Gyrus and Multimodal Feature Integration during Episodic and Semantic Memory Retrieval

In my first experimental chapter, I present a non-invasive brain stimulation study in which I tested the causal role of the left angular gyrus in multimodal feature integration during episodic and semantic memory retrieval. To this end, continuous theta burst stimulation was applied offline to left angular gyrus target and vertex control sites before the retrieval phase of a newly-designed associative memory task, to assess its effects on subsequent episodic associative recognition and semantic relatedness judgements made on the same unimodal and multimodal object pairs. Angular gyrus stimulation was found to selectively modulate response times in both episodic and semantic retrieval tasks, consistent with AnG-mediated multimodal integration during both forms of declarative memory retrieval. Contrary to predictions, however, this stimulation effect was facilitatory rather than inhibitory, and was not accompanied by differences in objective or subjective measures of episodic memory performance.

Introduction

Long-term declarative memory entails the conscious recall of personal events (i.e., episodic memory) and factual knowledge (i.e., semantic memory) (see Squire, 2004 for review). Much research has sought to dissociate episodic and semantic memory, yet work in more recent decades has highlighted increasing overlap in both their underlying cognitive processes and neural substrates (for reviews, see Binder et al., 2009; Brigard, Umanath, & Irish, 2022; Greenberg & Verfaellie, 2010; Humphreys et al., 2021; Irish & Piguet, 2013; Irish & Vatansever, 2020; Renoult et al., 2019). One fundamental feature of both forms of declarative memory is their fundamentally combinatorial nature, and several brain regions have been proposed as information convergence zones where such processing may occur. For example, the influential hub-and-spoke model of semantic memory holds the bilateral anterior temporal lobes as an amodal hub (i.e., representations can be received and expressed in any modality) that integrates sensory information of different modalities, represented in distributed modality-specific cortices or ‘spokes’, to form generalisable concepts (Patterson et al., 2007; Patterson & Lambon Ralph, 2016; Rogers et al., 2004; but see Bonner & Price, 2013). In the episodic memory literature, the hippocampus (HPC) of the medial temporal lobe has been advanced as a key subcortical structure supporting the associative/relational processing of contextual event information during episodic memory encoding (Olsen et al., 2012) and retrieval (Horner et al., 2015). However, another region of the brain, the left angular gyrus (AnG) of the posterior parietal cortex, has been linked to both episodic and semantic memory retrieval processes (for reviews, see Humphreys et al., 2021; Seghier, 2013). Moreover, the AnG is viewed as an ideal candidate for multisensory processing, being located near several sensory-motor processing streams and having reciprocal white matter and strong resting-state functional connectivity with modality-specific sensory association cortices (Seghier, 2013; Uddin et al., 2010).

Numerous functional neuroimaging reviews have implicated the left AnG in episodic memory retrieval (Rugg & King, 2018; Rugg & Vilberg, 2013; Sestieri, Shulman, & Corbetta, 2017; Wagner et al., 2005). The left AnG is a prominent member of the core-recollection network (Rugg & Vilberg, 2013; Kim, 2010), which along with the prefrontal cortex and temporal lobe structures such as the HPC, shows increased neural activity during successful recollection of contextual event details when compared against memory decisions based on the vague, acontextual sense of familiarity (Skinner & Fernandes, 2007; Thakral, Wang, & Rugg, 2017; Trelle, 2014; Vilberg & Rugg, 2008). The left AnG also belongs to the

default mode network (Buckner, Andrews-Hanna, & Schacter, 2008), which anatomically overlaps with the core recollection network and is characterised by increased resting-state connectivity during various introspective mental activities such as daydreaming, thinking about the past, or imagining the future. In remember/know tasks probing the subjective level of awareness accompanying episodic retrieval, “remember” responses reflecting the experience of recollection are associated with greater left AnG activity than familiarity-based “know” responses (Vilberg & Rugg, 2008). Greater left AnG engagement is also observed when the specific study context of items (i.e., source) is tested relative to when memory for the items themselves is tested (Vilberg & Rugg, 2008). Furthermore, memory for inter-item associations, which is similarly thought to primarily tap recollection, is associated with elevated left AnG activity (Chastelaine et al., 2016). Together, these data indicate the left AnG is involved in conscious episodic memory retrieval.

Curiously, patients with parietal lesions are typically not overtly amnesic, especially when retrieval is supported with cues (Berryhill et al., 2007; Simons et al., 2008; but see also Ben-Zvi, Soroker, & Levy, 2015). However, the subjective experience of recollection is often reported to be diminished in such patients (Ally et al., 2008; Simons et al., 2010; Hower et al., 2014). Compared against neurologically healthy age-matched controls, parietal lesion patients produce fewer “remember” responses in remember/know tasks (Davidson et al., 2008; Drowos et al., 2010) as well as describe less vivid recollection and report significantly reduced memory confidence (Simons et al., 2008; 2010). Similarly, transient disruption of left AnG function in neurologically healthy younger adults via inhibitory repetitive transcranial magnetic stimulation (TMS) reduces subjective source memory confidence while leaving objective source and item memory performance unaffected (Yazar, Bergström, & Simons, 2014). Inhibitory repetitive TMS also increases the perceived difficulty of episodic autobiographical memory and simulation tasks (Bonnici et al., 2018; Thakral, Madore, & Schacter, 2017) and alters source memory response bias (i.e., the tendency to provide a given source response regardless of the ability to accurately discriminate the source) (Sestieri et al., 2013). Such patient and non-invasive brain stimulation evidence has led to the proposal that the left AnG carries out processes necessary for the subjective experience of recollection (Ally et al., 2008; Moscovitch et al., 2016; Simons et al., 2022). Moreover, recent TMS evidence suggests the left AnG might mediate related metacognitive judgements (Sestieri et al., 2013) by possibly gauging the vividness of memory contents themselves (Zou & Kwok, 2022).

Activity in the left AnG often covaries with the amount of recollected visual or verbal episodic information (Bellana et al., 2019; Vilberg & Rugg, 2007; 2009a; 2009b). Consistent with this view, continuous measures of episodic memory have shown left AnG activity to scale with the visual fidelity of recollection (Richter et al., 2016). AnG activity has been shown to carry information about stimulus category and event-specific information. For example, individual visual episodic memories of common objects, faces, and scenes have variously been decoded from multivoxel patterns of fMRI activity in regions of the ventrolateral parietal cortex (VLPC) including the AnG (Favila et al., 2018; Kuhl & Chun, 2014; Lee & Kuhl, 2016). However, Kuhl & Chun (2014) speculated that such memory representations may not be purely visual. Further to this, univariate fMRI analysis of left AnG activity has also shown the region to be preferentially engaged during the recollection of multimodal audio-visual video clips versus recollection of unimodal audio or visual clips (Bonnici et al., 2016). Moreover, the left AnG shows greater recruitment during the retrieval of multimodal audio-visual than unimodal audio or visual pair associates, both when encoded intentionally (Tibon et al., 2019) and incidentally (Jablonowski & Rose, 2022). Multivoxel pattern analysis has additionally been used by Bonnici et al. (2016) to decode individual multimodal episodic memory representations within the left AnG, with classifier accuracy tracking the vividness of recollection. Finally, repetitive TMS of the left AnG has been shown to selectively disrupt the accuracy of source memory judgements on multimodal concurrent audio-visual scenes and not multiple or single scene features of the same modality (Yazar, Bergström, & Simons, 2017). Based on such findings, the left AnG is thought to play an important role in enabling the subjective experience of remembering by integrating sensory event features into richly detailed, holistic, multimodal episodic memory representations during retrieval (Simons, Ritchey, & Fernyhough, 2022).

Evidence from a traditionally separate body of work has suggested the left AnG might also be involved in semantic memory retrieval (for challenges to this view, see Humphreys et al., 2017; 2022; Humphreys, Jung, & Lambon Ralph 2022; Humphreys & Tibon, 2023, Lambon Ralph et al., 2017; but see also Kuhnke et al., 2023). Tasks involving the integration and retrieval of conceptual knowledge commonly elicit increased activity in VLPC (for reviews, see Binder et al., 2009; Binder & Desai, 2011; Price et al., 2015; Seghier, 2013). For example, difficult semantic relatedness judgements on auditorily presented word triplets are associated with increased activity in left AnG (Sharp et al., 2010). Activity in ventral left AnG is also modulated by semantic matching tasks in which participants search for shared

semantic features across pictures of objects or their written names (Seghier, Fagan, & Price, 2010). Furthermore, repetitive TMS applied to the left AnG disrupts word-to-picture matching, particularly when thematic associations are strong (Davey et al., 2015). In another brain stimulation study, high-definition anodal transcranial direct current stimulation of the left AnG has been shown to facilitate faster comprehension of semantically meaningful adjective-noun pairs versus nonsense pairs (Price et al., 2016). Finally, activity within the AnG covaries with the amount of semantic information that can be extracted from a given input (Binder, 2016), suggesting the representation of conceptual information.

In an early electroencephalography study in humans (Stein et al., 1999), the coherence in population activity between temporal and parietal cortices was shown to be enhanced during the presentation of objects across different stimulus modalities (i.e., pictures, spoken words, or written words), which was interpreted as indicating the binding of multimodal semantic entities into supramodal representations. In more recent fMRI studies, AnG activity has been associated with semantic categories of varying sensory-motor features during retrieval (Bonner et al., 2013; Démonet et al., 1992; Price et al., 2015; Stein et al., 1999; Vandenberghe et al., 1996). Such findings, and those from the episodic memory literature, raise the question as to whether the left AnG integrates multimodal information across different forms of declarative memory retrieval. As noted previously, the AnG is anatomically well suited for performing such processing, perhaps contributing to the broad, integrated representation of concepts in the case of semantic retrieval (Binder & Desai, 2011; Bonner et al., 2013; Seghier, 2013). Under the parietal unified connectivity-biased computation (PUCC) model (Humphreys & Lambon Ralph, 2015; Humphreys, Lambon Ralph, & Simons, 2021; Humphreys & Tibon, 2022), the AnG may achieve integrative semantic processing via the domain-general temporary buffering of spatiotemporal information. Typically, parietal activity that is shared across unimodal stimuli of different sensorimotor categories has been interpreted as evidence for multimodal semantic processing. However, it can be argued that such data are inconclusive as comparison with truly multimodal stimuli is needed to adequately test this view.

Considering the above limitations, Bonnici et al. (2016) investigated whether left AnG supports multimodal feature integration during episodic and semantic memory retrieval by contrasting fMRI activity elicited by unimodal and multimodal stimuli in corresponding retrieval tasks. In the episodic retrieval task, participants mentally replayed multimodal audio-visual video clips and unimodal audio or silent visual clips. In the semantic retrieval

task, participants generated word associations to unimodal and multimodal cues. Consistent with the multimodal feature integration account, multimodal episodic retrieval was associated with significantly greater activity in the left AnG than unimodal episodic retrieval. However, the left AnG was activated to a statistically equivalent degree under both unimodal and multimodal semantic retrieval conditions. One explanation for this finding is that semantic representations within the AnG may be amodal in nature and thus lack sensory detail. However, this seems inconsistent with the causal evidence for its role in integrating multisensory features during episodic memory retrieval (Yazar, Bergström, & Simons, 2017). Alternatively, semantic memories may be inherently multimodal, reactivating assorted sensory-perceptual associations regardless of presentation modality. This explanation also seems unlikely, however, given that unimodal semantic memories activated distinct unisensory cortical regions, which were activated to an intermediate degree during multimodal semantic retrieval. Yet another possibility is that the modality manipulation did not affect both retrieval tasks. Indeed, the modality of semantic retrieval was not explicitly controlled by Bonnici et al., despite screening the word association stimuli for dominance in one or both sensory modalities. Therefore, the activation differences observed in their study might simply have reflected differences in the materials used to probe episodic and semantic retrieval.

The study presented in the current chapter used non-invasive brain stimulation to test whether the left AnG plays a causal role in multimodal feature integration during episodic and semantic retrieval. A within-subjects design was employed in which the effects of continuous theta burst stimulation (cTBS; Huang et al., 2005), applied offline either to the left AnG or a vertex control site, were examined on performance in a custom associative memory task that manipulated stimulus modality. Critically, this task format permitted both associative recognition and semantic relatedness judgements to be made on the same tested pair associates, thereby permitting episodic and semantic memory retrieval to be assessed using the same materials. Moreover, these episodic and semantic retrieval tasks were selected based on their shared emphasis on integrative processing. As with other variants of repetitive TMS, cTBS can establish which brain regions are necessary for task performance by interfering with the neural processing therein. Based on previous neuroimaging evidence for left AnG involvement in multimodal integration during episodic (Bonnici et al., 2016; see also Jablonowski & Rose, 2022; Tibon et al., 2019) and possibly semantic memory retrieval (Bonnici et al., 2016), it was predicted that left AnG cTBS would increase response latencies

in multimodal but not unimodal trials of the corresponding retrieval tasks, relative to vertex control stimulation. Additionally, given the proposed importance of multimodal episodic feature retrieval in enabling the subjective reliving of past experiences (Simons, Ritchey, & Fernyhough, 2022), left AnG cTBS was predicted to selectively disrupt both multimodal accuracy (Yazar, Bergström, & Simons, 2017) and confidence (Yazar, Bergström, & Simons, 2014) in the associative recognition task.

Materials and Methods

Participants

23 right-handed young adults aged 19 – 34 years ($M = 26.13$, $SD = 4.40$) were tested and analysed. A further six participants were tested but excluded from analysis owing to chance-level performance, excessive anticipatory responses, or technical issues with the TMS system. A seventh participant was excluded after reporting an unusually elevated mood, tingling sensations, and involuntary twitching approximately 35 hours following vertex stimulation in their second session. These symptoms abated soon thereafter. This participant had previously completed another cTBS study without incident and, as with all participants, established safety protocols were adhered to in the present study (for details, see cTBS procedure section). All participants were screened for contraindications to TMS and none reported current or historical diagnoses of developmental, psychiatric, or neurological conditions. Additionally, all participants reported native-like English proficiency and had normal or corrected-to-normal vision and hearing. Participants also gave written informed consent before beginning the study and were remunerated for participating in a manner approved by the University of Cambridge Human Biology Research Ethics Committee.

Stimuli

Stimuli were 256 unique common objects presented as 128 colour line drawings and 128 short audio clips. The pictorial stimuli were a subset of those used by Tibon & Levy (2014), had a 256 x 256-pixel resolution, and occupied a 3-in screen area on a 17-in computer display with a 1920 x 1080-pixel resolution. The auditory stimuli were sourced from the Internet and represented typical sounds associated with common objects (e.g., a car horn blaring, a dog barking, or a guitar being strummed). These stimuli were processed using Audacity audio editing software (v2.1.3; <https://github.com/audacity/audacity/releases/tag/Audacity-2.1.3>) to normalise volume, trim length to 4 seconds (s), and equate the sample rate and bit depth to 44 kHz and 16 bits, respectively. Additionally, these stimuli were presented binaurally via headphones along with

an on-screen speaker icon of equivalent dimensions to the pictorial stimuli. The objects represented by these auditory stimuli were identified with a mean accuracy of 97% (SD = 7%) by an independent set of raters ($n = 6$).

Task procedure

In a within-subjects design, participants performed the same episodic and semantic retrieval tasks on object pairs in two different sessions: one experimental (i.e., AnG stimulation) and one control (i.e., vertex stimulation). Session order (and therefore, stimulation site) was counterbalanced across participants. These sessions were spaced at least 48 hours apart to minimise potential stimulation carryover effects. The mean inter-session interval was 5.42 days (SD = 2.21 days, range = 2 – 12 days). At the start of each session, participants were instructed on the memory task, which they also practiced. The main task followed and involved a single testing block consisting of an initial study phase, a short break, and then a test phase (see Figure 1 for a schematic illustration). In short, the study phase involved memorising pairs of objects, whose presentation modality was manipulated. During the break, participants received brain stimulation and completed a perceptual distractor task. Finally, in the test phase, participants made episodic associative recognition and semantic relatedness judgements on pairs of studied objects, which either remained in their original pairings or were rearranged using objects from different studied pairs. The task was coded in MATLAB 2017b (The MathWorks), and stimuli were presented using the ‘Psychophysics Toolbox’ (v3.0.14; <http://psychtoolbox.org/download.html>).

In the study phase, participants memorised pairs of common objects. A separate behavioural pilot study ($n = 18$ participants) was conducted to adjust associative recognition task difficulty by varying the number of studied object pairs, which resulted in 64 study trials per session. The beginning of each study trial was indicated with the presentation of a red fixation cross in the centre of the screen for 1s. Next, two different objects comprising a pair were presented in the following sequence: the first object for 4s, followed by a black central fixation cross for 500ms, then the second object for another 4s. Presentation modality was split equally across object pairs, yielding 32 unimodal (i.e., composed of 16 audio-audio and 16 visual-visual object pairs) and 32 multimodal (i.e., 16 audio-visual and 16 visual-audio object pairs) study trials per session. In the final stage of study trials, participants had up to 10s before timeout to encode each object pair by pressing the ‘z’ and ‘m’ keyboard keys to indicate whether the first or second object was bigger in real life. The order of study trials was pseudorandomised so that no more than three trials of the same type were repeated.

After completing the study phase, participants had a 10-minute break during which they received brain stimulation. Earlier pilot work indicated a study-test interval of this length was necessary to bring associative recognition performance down from ceiling to an acceptable level. Participants spent the first five minutes of the break reading a magazine or book, which they were instructed to bring in advance. This was intended to discourage rehearsal of studied object pairs in working memory. Once five minutes had elapsed, cTBS was then delivered either to the left AnG or a vertex control site, depending on the session counterbalancing. Following brain stimulation, participants were instructed to spend the remaining minutes of the break copying either a Rey–Osterrieth or Modified Taylor complex figure as precisely as they could by eye. These perceptual tasks were administered post-stimulation, before participants began the test phase, to ensure that all were engaged in the same non-memory related activities before performing the retrieval tasks. While perceptual copy difficulty is thought to be comparable for these complex figures (Hubley & Tremblay, 2002; but see Hubley, 2010), their order was nevertheless counterbalanced across participants.

During the test phase, participants made episodic associative recognition and semantic relatedness judgements on pairs of the objects they studied earlier in the session. As in the study phase, test trials started with the presentation of a red central fixation cross for 1s. A unimodal or multimodal object pair was then presented in sequence (also as in the study phase). However, only half these objects remained in their studied pairings (i.e., 32 intact trials). The other half were recombined using objects from different studied pairs of the same presentation modality (i.e., 32 rearranged trials). Like the study phase, presentation modality was divided equally among intact and rearranged trials (i.e., both comprised 16 unimodal and 16 multimodal objects pairs). After an object pair was presented, prompts for the associative recognition and semantic relatedness judgements were displayed one after the other. This permitted both forms of declarative memory retrieval to be assessed using the same materials. However, as one form of retrieval might subsequently affect the other, the order of these retrieval tasks was counterbalanced across participants. The two retrieval task prompts were separated by a 500ms-long black central fixation cross, and both remained onscreen until a response was given or the 10s response deadline was reached. The associative recognition judgements required participants to rate their level of confidence that an object pair had remained intact or was rearranged. To encourage more effortful processing, semantic relatedness judgements involved rating the degree to which the objects presented at test were

related to one another. Responses were made using a six-point scale that was displayed below both retrieval task prompts. For the associative recognition task, this corresponded to 1 = “definitely intact”, 2 = “maybe intact”, 3 = “guessing intact”, 4 = “guessing rearranged”, 5 = “maybe rearranged”, and 6 = “definitely rearranged”. By contrast, the scale used for the semantic relatedness task ranged from 1 (“very unrelated”) to 6 (“very related”). As in the study phase, test trial order was pseudorandomised.

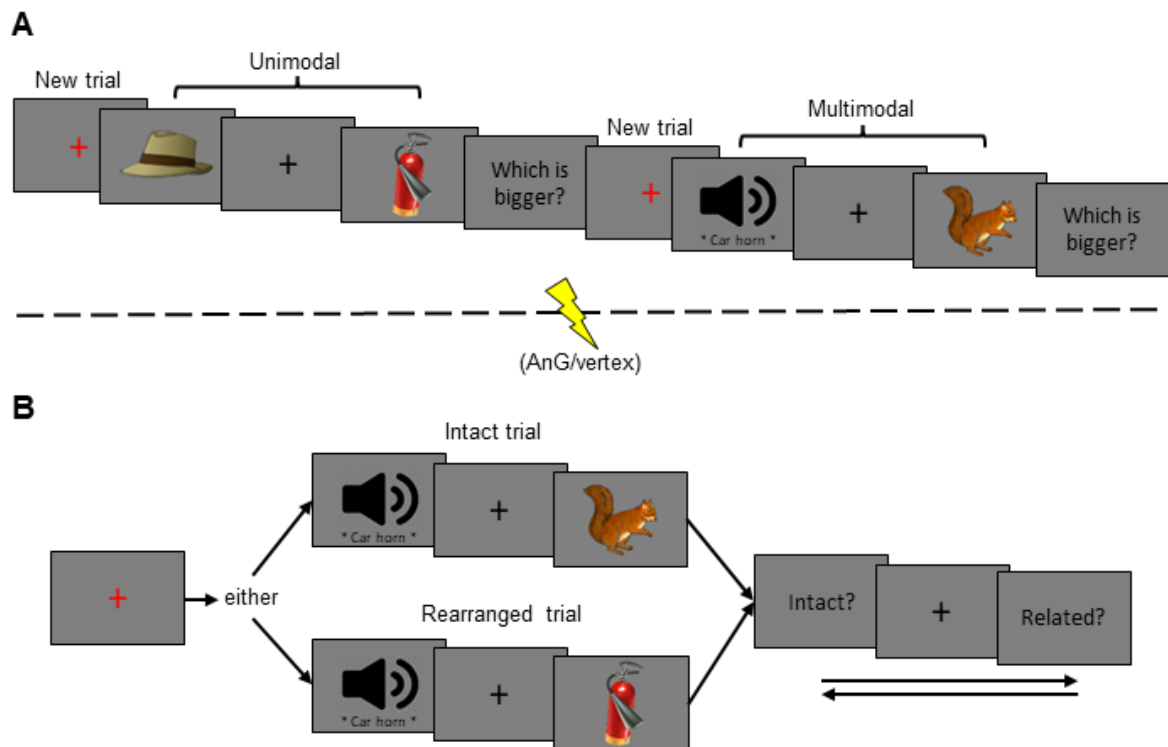


Figure 1. Schematic illustration of the memory task. A) First, participants studied pairs of sequentially presented objects in the study phase. These object pairs were presented either as two images or two sounds (i.e., unimodal) or a combination of the two (i.e., multimodal). Halfway through a 10-minute break cTBS was delivered either to the left AnG or a vertex control site to disrupt subsequent declarative memory retrieval. B) During the test phase, participants made episodic associative recognition and semantic relatedness judgements on the same intact and rearranged object pairs. Note that text within the displays has been abbreviated for clarity.

cTBS procedure

Neuronavigation was performed using aBrainsight computerised frameless stereotaxic system (Rogue Research, Canada) and Polaris Vicra optical 3D tracking system (Northern Digital, Canada). Each participant’s T1-weighted structural MRI head scan was prepared ahead of the testing sessions using the Brainsight software. First, the anterior and posterior commissures were manually identified, and a bounding box was adjusted to fit the

edges of each brain. This enabled automatic conversion between native participant space and standard Montreal Neurological Institute (MNI) space using an affine transformation. Anatomical landmarks consisting of the nasal tip, nasion, and bilateral preauricular areas were then identified on each participant's scan to aid later co-registration. Finally, TMS coil trajectories for each stimulation target site were set and optimised using theBrainsight trajectory tool.

At the beginning of each testing session, participants were co-registered to their MRI scan via the pre-defined anatomical landmarks. The mean co-registration error measured across sessions was 3.87mm (SD = 2.45, range = 2 – 10mm). Following co-registration in the first session, the resting motor threshold (RMT) of each participant was assessed using an adaptive threshold-hunting approach based on maximum likelihood estimation (TMS Motor Threshold Assessment Tool 2.0; <https://www.clinicalresearcher.org/software.htm>). Motor responses were defined as an involuntary twitch of the right index finger or thumb induced by single TMS pulses, which were applied to the motor cortex (and experimental sites) using a Magstim Rapid² stimulator and a 70mm figure-of-eight TMS coil. Where motor responses could not be elicited ($n = 7$ participants), 70% of the maximum stimulator output substituted the RMT. The intensity of stimulation did not exceed this figure at any point during the study.

Both the left AnG and a vertex control site were stimulated in the main experiment. The left AnG target site (MNI = [-43, -66, 38]) was centred on a recollection-sensitive VLPC fMRI activation cluster from an influential meta-review of the parietal lobe and memory (Vilberg & Rugg, 2008). Furthermore, TMS of this coordinate has previously been demonstrated to disrupt multimodal episodic memory retrieval (Yazar, Bergström, & Simons, 2017). This coordinate is also located near a left AnG peak fMRI coordinate associated semantic integration during narrative reading (Branzi et al., 2020), which was recently shown to be disrupted with online TMS (Branzi et al., 2021). The vertex control site (MNI = [0, -15, 74]) was derived from a probabilistic anatomical atlas (Okamoto et al., 2004). This region is often chosen as an active stimulation control site in TMS studies of memory due to its apparent lack of involvement in relevant processes (see Yeh & Rose, 2019 for review).

Both experimental sites were administered a standard cTBS conditioning protocol consisting of 600 TMS pulses delivered offline in 50Hz triplets repeated at 200ms intervals for 40s (Huang et al., 2005). This protocol is thought to suppress post-stimulation cortical excitability for up to 60 minutes through the modulation of long-term depression-like

plasticity mechanisms (Huang et al., 2005; Huang et al., 2011; Lazzaro et al., 2005), making cTBS well suited for investigating long-term memory retrieval processes. To ensure that stimulation effects were maximal during memory retrieval, cTBS was administered five minutes before the test phase (Huang et al., 2005). Additionally, cTBS dosage was individualised for each participant at 70% of their RMT as is typical for studies of this kind (Bonnici et al., 2018; Kwon et al., 2022; Yazar, Bergström, & Simons, 2014; 2017). Thus, cTBS had a mean intensity of 45% of the maximum stimulator output (SD = 5%, range = 35 – 49%). During cTBS administration, the centre of the TMS coil deviated from the left AnG target site by no more than 2.36mm (M = 1.13mm, SD = 0.57mm). All TMS procedures followed established safety guidelines (Rossi et al., 2009; 2021).

Behavioural measures and analysis

The main analysis concentrated on median semantic relatedness RT (in ms) in the semantic relatedness task and median RT (in ms) of correct responses in the associative recognition task (i.e., correctly identified intact pairs and correctly rejected rearranged pairs). These tasks were analysed separately. Further analysis was conducted on mean response bias-corrected associative recognition accuracy (Pr) and mean associative recognition memory confidence level. Pr was computed as the proportion of correctly identified intact pairs (i.e., hit rate) minus the proportion of rearranged pairs incorrectly identified as intact (i.e., false alarm (FA) rate). The resulting score ranges from 0 to 1, with a value of 0 indicating chance level performance. Memory confidence was defined as the proportion of high confidence correct responses (i.e., “definitely intact” or “definitely rearranged” responses), analogous to the operationalisation of confidence in Yazar, Bergström, & Simons (2014). Associative recognition performance was further examined with the analysis of separate signal detection theory-derived parametric measures of recognition discriminability (d') and response bias (C). d' indexes the ability to distinguish between intact and rearranged object pairs (i.e., sensitivity) and was calculated as the difference between z-transformed hit and FA rates. Additionally, a Hautus (1995) adjustment was applied to d' to account for extreme values. A d' value of 0 indicates an inability to distinguish intact from rearranged object pairs, whereas increasingly larger d' values indicate a correspondingly greater ability to do so. By contrast, C provides complementary information to d' by capturing the tendency to endorse object pairs as intact or rearranged, which was defined as the midpoint between z-transformed hit and FA rates. A C value of 0 indicates an absence of response bias, whereas positive or negative values reflect respective biases toward responding “intact” or “rearranged”. Data

were minimally pre-processed in general to reduce Type-I error (Morís Fernández & Vadillo, 2020), with only anticipatory responses (RTs < 300ms) and timed out trials being discarded (1.5% of all semantic relatedness trials and 2% of all associative recognition trials).

All analyses were performed using R Statistical Software (version 4.1.2; R Foundation for Statistical Computing, Vienna, Austria). Signal detection theory-based measures were computed using the ‘psycho’ R package (v0.6.1; Makowski, 2018). Repeated measures analysis of variance (ANOVAs) with the factors *site* (AnG, vertex) and *modality* (unimodal, multimodal) was conducted on all measures using the ‘ez’ package (v4.4-0; Lawrence, 2016). Power analysis using G*Power (v3.1.9.4; Faul et al., 2007; 2009) estimated a sample size of 24 was needed to detect a medium effect size in these analyses ($f = 0.25$, $\alpha = 0.05$, $1 - \beta = 0.80$). This sample size is comparable to those used in other within-subject design TMS studies on AnG memory function (Bonnici et al., 2018; Koen, Thakral, & Rugg, 2018; Thakral, Madore, & Schacter, 2017; Yazar, Bergström, & Simons, 2017; Zou & Kwok, 2022). Sphericity was assumed for all repeated measures ANOVAs as no factor had more than two levels. The assumptions of residual normality and homogeneous error variance were evaluated using standard diagnostic residual plots. Data were transformed where these assumptions were violated. The interquartile range method was used to identify outliers (i.e., values greater than 1.5x the interquartile range) as it makes no distributional assumptions. All tests were two-tailed at a standard alpha level of 0.05 and *p*-values are reported to three decimal places (unless $p < 0.001$). Complementary partial Eta squared (η^2_p) and Cohen’s *d* standardised effect sizes with 95% confidence intervals (CIs), computed using the ‘effectsize’ package (v0.6.0.1; Ben-Shacher, Lüdtke, & Makowski, 2020), are also provided where appropriate.

Results

Semantic relatedness and associative recognition response time

First, to assess the effect of AnG cTBS on multimodal semantic integration, a two-way repeated measures ANOVA was conducted on semantic relatedness RTs (see Table 1 for summary statistics). There was a significant main effect of *modality* ($F(1, 22) = 6.31$, $p = 0.020$, $\eta^2_p = 0.22$, 95% CI [0.02, 0.49]) but not *site* ($F(1, 22) = 0.13$, $p = 0.725$, $\eta^2_p < 0.01$, 95% CI [0.00, 0.21]). Consistent with a selective stimulation effect, the *site* x *modality* interaction was significant ($F(1, 22) = 6.51$, $p = 0.018$, $\eta^2_p = 0.23$, 95% CI [0.01, 0.49]). This interaction was decomposed with follow-up paired-sample *t*-tests on *modality* at both levels of *site*. Semantic relatedness RTs did not significantly differ by modality under vertex cTBS

($t(22) = 0.13$, $p = 0.898$, $d = 0.03$, 95% CI [-0.39, 0.45]). By contrast, AnG cTBS significantly decreased multimodal versus unimodal semantic relatedness RTs ($t(22) = 3.29$, $p = 0.003$, $d = 0.69$, 95% CI [0.23, 1.16]), indicating stimulation-induced facilitation (rather than predicted inhibition) of multimodal semantic relatedness responses (see Figure 2, left).

Table 1. Mean (SD in brackets) RT for the associative recognition and semantic relatedness tasks.

Modality	Vertex		AnG	
	Recognition	Relatedness	Recognition	Relatedness
Unimodal	1344.91 (563.51)	2017.80 (597.63)	1489.64 (799.21)	2077.81 (862.59)
Multimodal	1389.49 (607.38)	2009.91 (684.34)	1333.56 (624.85)	1837.22 (764.45)

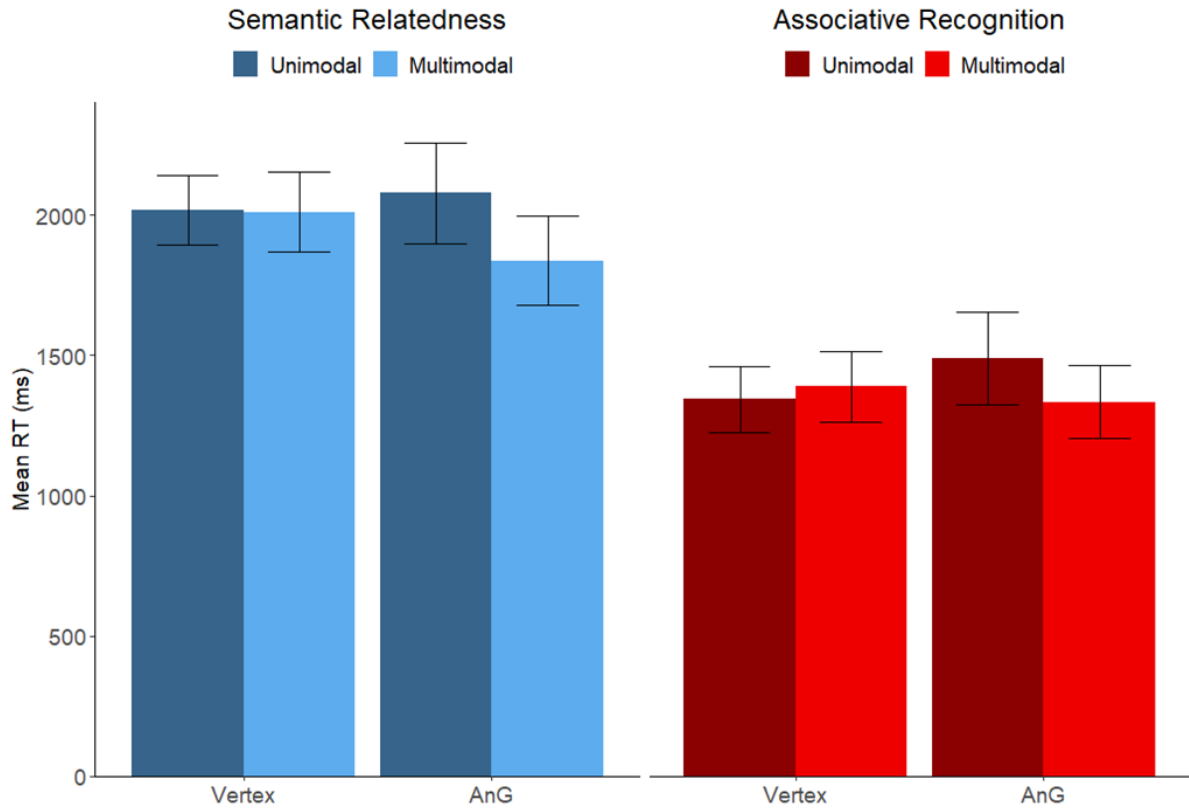


Figure 2. Mean unimodal and multimodal semantic relatedness (left) and associative recognition (right) median RTs following vertex and left AnG cTBS. Error bars represent standard error of the mean.

Next, the effect of brain stimulation on multimodal integration during episodic retrieval was investigated with a two-way repeated measures ANOVA on associative recognition RTs. There were no significant main effects of *site* ($F(1, 22) = 0.13$, $p = 0.725$, $\eta^2_p < 0.01$, 95% CI [0.00, 0.19]) or *modality* ($F(1, 22) = 2.03$, $p = 0.169$, $\eta^2_p = 0.08$, 95% CI

[0.00, 0.35]). As in the semantic relatedness RT analysis, however, the *site x modality* interaction was significant ($F(1, 22) = 4.49, p = 0.046, \eta^2_p = 0.17, 95\% \text{ CI } [0.00, 0.44]$). Based on the width of the CIs, it should be cautioned that the true population effects could not be reliably estimated from these data, possibly due to small sample size. The significant interaction was followed up on with paired samples *t*-tests on *modality*, conditioned on *site*. Associative recognition RTs did not significantly differ by modality following vertex stimulation ($t(22) = -1.21, p = 0.239, d = -0.25, 95\% \text{ CI } [-0.68, 0.17]$). Under AnG cTBS, however, the difference between unimodal and multimodal associative recognition RTs was not significant ($t(22) = 1.98, p = 0.060, d = 0.41, 95\% \text{ CI } [-0.02, 0.85]$; see Figure 2, right).

Several outlier RT observations (range = 2273.10 - 4245.40ms) that could not be attributed to error were detected in the full associative recognition RT dataset. To check the robustness of the results of the main analysis of this task, a sensitivity analysis was conducted in which subjects contributing these outliers were excluded ($n = 3$). In this analysis, the *site x modality* interaction lost significance ($F(1, 19) = 2.14, p = 0.160, \eta^2_p = 0.10, 95\% \text{ CI } [0.00, 0.39]$), suggesting the stimulation effect observed for associative recognition RTs was driven by a few subjects. As in the main analysis, no significant main effect of *modality* ($F(1, 19) = 0.83, p = 0.373, \eta^2_p = 0.04, 95\% \text{ CI } [0.00, 0.30]$) or *site* ($F(1, 19) = 0.58, p = 0.454, \eta^2_p = 0.03, 95\% \text{ CI } [0.00, 0.28]$) was found.

It should also be noted that the residual plots for the analysis of raw associative recognition RTs showed noteworthy positive skew and possible heteroscedasticity. As ANOVAs are not robust to assumption violations in small samples (Oberfeld & Franke, 2013), these concerns were addressed by logarithmically transforming associative recognition RT, which stabilised residual variance and reduced skew. Contrary to the analysis of raw associative recognition RTs, the two-way repeated measures ANOVA on associative recognition $\log_{10}$ -RT did not reveal a significant *site x modality* interaction ($F(1, 22) = 2.40, p = 0.135, \eta^2_p = 0.10, 95\% \text{ CI } [0.00, 0.36]$), consistent with the absence of a selective stimulation effect on RTs in this scale. Neither the main effect of *site* ($F(1, 22) = 0.04, p = 0.848, \eta^2_p < 0.01, 95\% \text{ CI } [0.00, 0.14]$) nor *modality* ($F(1, 22) = 1.11, p = 0.304, \eta^2_p = 0.05, 95\% \text{ CI } [0.00, 0.29]$) was significant.

Visual inspection of Figure 2 indicated possible speeding of multimodal semantic relatedness RTs and slowing of unimodal associative recognition RTs following AnG stimulation. This possibility was explored via post-hoc tests in both retrieval tasks to compare

the effects of AnG versus vertex stimulation within each stimulus modality. These analyses revealed no significant differences in unimodal ($t(22) = -0.435$, $p = 0.668$, $d = -0.09$, 95% CI [-0.51, 0.33]) or multimodal ($t(22) = 1.426$, $p = 0.168$, $d = 0.30$, 95% CI [-0.13, 0.73]) semantic relatedness RTs following AnG stimulation. Likewise, there were no significant differences in unimodal ($t(22) = -0.962$, $p = 0.346$, $d = -0.20$, 95% CI [-0.63, 0.22]) or multimodal ($t(22) = 0.492$, $p = 0.628$, $d = 0.10$, 95% CI [-0.32, 0.52]) associative recognition RTs after AnG stimulation.

Finally, exploratory correlation analyses were run in both retrieval tasks to test whether the strength of the RT effects, defined as the difference score between multimodal and unimodal RT under AnG stimulation, was correlated with the level of stimulation. Rank-based Kendall correlations were chosen to account for the right-skewed distribution of cTBS intensity delivered to participants. This correlation was not significant in the semantic relatedness task ($\tau_b < 0.01$, $p = 0.978$) or in the associative recognition task ($\tau_b = 0.27$, $p = 0.087$).

Associative recognition performance and confidence

Turning to associative recognition task performance (see Table 2 for descriptive statistics), the two-way repeated measures ANOVA on response-bias corrected accuracy (Pr) did not find a significant *site* x *modality* interaction ($F(1, 22) = 0.02$, $p = 0.895$, $\eta^2_p < 0.01$, 95% CI [0.00, 0.12]) or significant main effects of *site* ($F(1, 22) = 0.18$, $p = 0.679$, $\eta^2_p < 0.01$, 95% CI [0.00, 0.20]) or *modality* ($F(1, 22) = 0.89$, $p = 0.356$, $\eta^2_p = 0.04$, 95% CI [0.00, 0.28]). An additional exploratory two-way repeated measures ANOVA was performed on the correct rejection (CR) rate based on observed numeric patterns of performance consistent with predictions. However, no significant *site* x *modality* interaction ($F(1, 22) = 0.70$, $p = 0.41$, $\eta^2_p = 0.03$, 95% CI [0.00, 0.26]), main effect of *site* ($F(1, 22) = 0.09$, $p = 0.77$, $\eta^2_p < 0.01$, 95% CI [0.00, 0.17]), or main effect of *modality* ($F(1, 22) = 0.49$, $p = 0.49$, $\eta^2_p = 0.02$, 95% CI [0.00, 0.24]) was revealed.

Table 2. Mean (SD in brackets) performance measures for the associative recognition task.

Modality	Vertex				AnG			
	Pr	d'	C	Conf.	Pr	d'	C	Conf.
Unimodal	0.60	1.87	0.10	0.53	0.59	1.76	0.14	0.51
	(0.20)	(0.83)	(0.42)	(0.16)	(0.18)	(0.73)	(0.31)	(0.17)
Multimodal	0.57	1.77	0.15	0.51	0.55	1.71	0.10	0.51
	(0.22)	(0.89)	(0.34)	(0.18)	(0.21)	(0.80)	(0.44)	(0.15)

The two-way repeated measures ANOVA on memory confidence found no significant *site x modality* interaction ($F(1, 22) = 0.1204, p = 0.732, \eta^2_p < 0.01, 95\% \text{ CI } [0.00, 0.18]$), main effect of *site* ($F(1, 22) = 0.4942, p = 0.490, \eta^2_p = 0.02, 95\% \text{ CI } [0.00, 0.24]$), or main effect of *modality* ($F(1, 22) = 0.35, p = 0.561, \eta^2_p = 0.02, 95\% \text{ CI } [0.00, 0.24]$). As the *a priori* analysis of memory confidence was restricted to high confidence correct responses (Yazar, Bergström, & Simons, 2014), further analyses were conducted to explore possible effects of AnG cTBS on alternative formulations of memory confidence. However, no significant main effects or interactions were found when examining the proportion of high confidence responses irrespective of accuracy, overall guess rate, or any confidence measure separated by intact and rearranged trial types (all $F_s < 1.76$ and all $p_s > 0.198$).

Next, the effects of AnG cTBS on separate measures of associative recognition discriminability (d') and response bias (C) were examined. Mirroring the previous analyses, the two-way repeated measures ANOVA on d' , neither the *site x modality* interaction ($F(1, 22) = 0.06, p = 0.802, \eta^2_p < 0.01, 95\% \text{ CI } [0.00, 0.16]$) nor the main effects of *site* ($F(1, 22) = 0.32, p = 0.580, \eta^2_p = 0.01, 95\% \text{ CI } [0.00, 0.22]$) and *modality* ($F(1, 22) = 0.26, p = 0.618, \eta^2_p = 0.01, 95\% \text{ CI } [0.00, 0.21]$) were significant. The two-way repeated measures ANOVA on C similarly showed no significant *site x modality* interaction ($F(1, 22) = 0.49, p = 0.490, \eta^2_p = 0.02, 95\% \text{ CI } [0.00, 0.24]$) or main effects of *site* ($F(1, 22) = 0.01, p = 0.94, \eta^2_p < 0.01, 95\% \text{ CI } [0.00, 0.07]$) or *modality* ($F(1, 22) < 0.01, p = 0.974, \eta^2_p < 0.01, 95\% \text{ CI } [0.00, 0.00]$). Excluding subjects from whom no motor response could be elicited ($n = 7$) did not change the results of any of the associative recognition analyses reported here or the overall pattern of results in the main RT analyses.

Recent evidence indicates substantial interindividual variability in response to theta burst stimulation (Corp et al., 2020; Jannati et al., 2017; Lowe & Hall, 2018), which might have masked genuine stimulation effects in the current study. To address this concern, associative recognition task performance and confidence were re-analysed according to the direction of the AnG cTBS effect based on associative recognition RT. This was determined for each participant by computing the difference score between multimodal and unimodal RT under AnG stimulation (see Figure 3 for subject plot). Participants with slower multimodal than unimodal RT were considered to show an inhibitory effect whereas those with comparatively faster multimodal RT were classed as showing a facilitatory effect. When analysed separately, neither subgroup showed a significant *site x modality* interaction for any measure (all $F_s < 0.18$ and all $p_s > 0.225$). These exploratory results and those from the main

analysis indicate that AnG cTBS had little overall effect on associative recognition task performance and confidence.

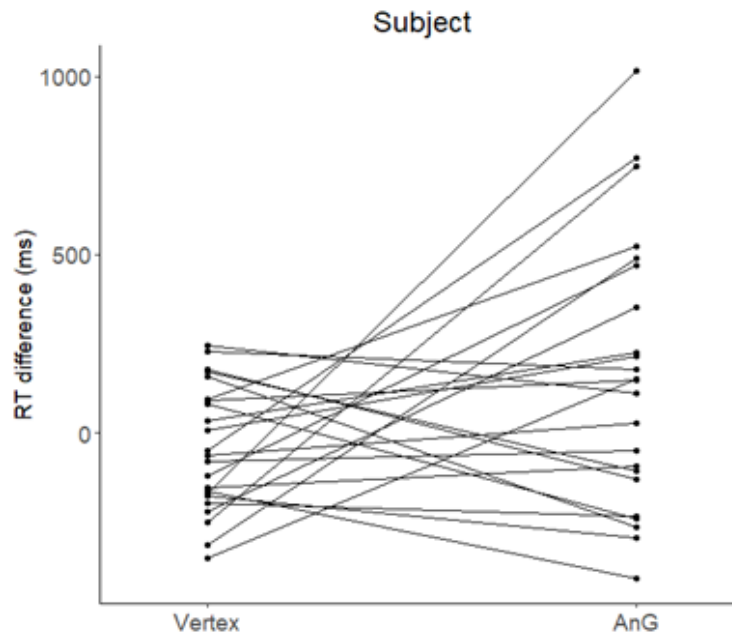


Figure 3. By-subject modality difference scores for associative recognition RTs following vertex and left AnG cTBS.

To account for potential interindividual variability in cTBS effects, the trial-level data for the associative recognition task ($n = 2,888$ observations) were submitted to a binomial linear mixed model, implemented in the ‘lme4’ package (Bates et al., 2015). Responses in each trial were coded dichotomously as correct/incorrect. This model included fixed factors of *site* and *modality*, which were represented using an effects coding scheme to permit an ANOVA-like interpretation of results (Singmann & Kellen, 2019). As the trial-level data did not support the maximal random effects structure, random effects were eliminated in the manner recommended by Barr et al. (2013) to prioritise capturing interindividual variability in the *site* $\times$ *modality* interaction of interest (i.e., the stimulation effect). This resulted in by-subject random slopes only for the interaction and not the main effects or intercept (model specification in lme4 syntax: `isTrialCorrect ~ site * modality + (0 + site : modality | subject)`). The binomial model on trial-level associative recognition performance had a significant intercept ($\beta = 1.48$, $SE = 0.10$, $z = 14.26$, $p < 0.005$). As in the subject-level analyses, however, the *site* $\times$ *modality* interaction remained non-significant after accounting for interindividual variability in the stimulation effect ($\beta = -0.01$, $SE = 0.05$, $z = -0.13$, $p = 0.90$). There were no significant main effects of *site* ($\beta = -0.04$, $SE = 0.06$, $z = -0.68$, $p = 0.49$) or *modality* ($\beta = -0.05$, $SE = 0.06$, $z = -0.89$, $p = 0.37$) either.

As the AnG is thought to support detailed recollection, the cTBS manipulation might have failed to modulate associative recognition task performance in the present study due to participants relying more on acontextual familiarity-based responses. While associative recognition judgements are typically based on recollection (Yonelinas et al., 2010), familiarity may also contribute when associates are processed as a single unit during encoding (i.e., unitized; Graf & Shacter, 1989). This possibility was graphically explored by examining receiver-operating characteristic (ROC) curves, which plot hit and false alarm rates against increasingly strict response criteria (here, confidence level). According to the influential dual-process signal detection model (DPSD; Yonelinas, 1994), recognition memory is supported by separable threshold-based and strength-based memory processes (i.e., recollection and familiarity, respectively). Under the DPSD model, recollection and familiarity are predicted to produce different ROC curves: responses based exclusively on familiarity lead to a symmetrical, curvilinear ROC curve whereas exclusively recollection-based responses lead to a mostly linear, ‘hockey-stick’-shaped ROC curve (for reviews, see Yonelinas & Parks, 2007; Yonelinas et al., 2010). However, a mixture of these two ROC curves is often observed, ostensibly reflecting the combined contributions of both processes to recognition memory. In this case, the intercept indexes recollection whereas the degree of curvilinearity provides a measure of familiarity. In the present study, a symmetrical and curvilinear ROC curve was found across stimulation sites and modality conditions, which is consistent with predominantly familiarity-based recognition judgements (see Figure 4).

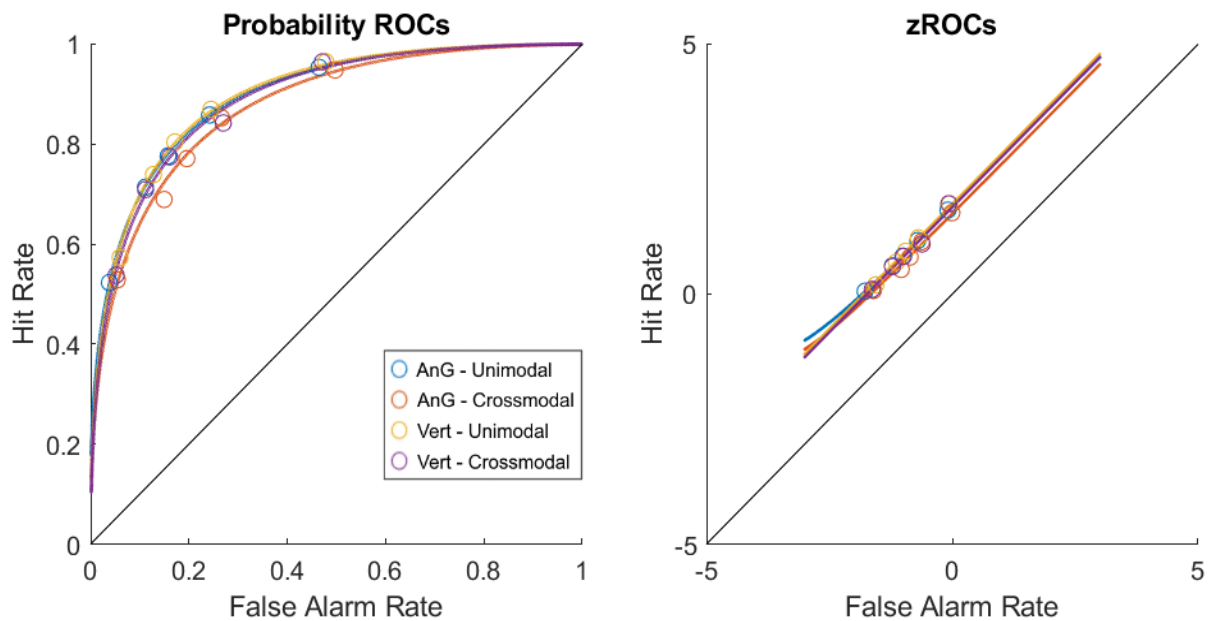


Figure 4. ROC curves in probability space (left) and standardised z-space (right) for each stimulation site and modality condition. These plots were created in MATLAB using ‘ROC Toolbox’ (v1.1.4; https://github.com/jdkoen/roc_toolbox; Koen et al., 2017).

Discussion

The study presented in this chapter used cTBS and a custom associative memory task that varied stimulus modality to test whether the left AnG plays a causal role in multimodal integration during both episodic and semantic memory retrieval. Critically, stimulus modality was manipulated while holding the number of objects in each pair constant across conditions. This allowed the distinction between general feature integration and more specific multimodal feature integration to be drawn. Relative to vertex control stimulation, left AnG cTBS modulated multimodal RT in both episodic and semantic retrieval tasks, consistent with the domain-general integration of multimodal information during declarative memory retrieval. Contrary to predictions, however, left AnG cTBS was found to facilitate rather than inhibit RT. Additionally, left AnG cTBS did not significantly affect objective measures of associative recognition performance or subjective memory confidence measures, indicating a weak overall stimulation effect. These null results may be explained by insufficient statistical power, although the sample size collected in the present study was in line with *a priori* power estimations and those of similar cTBS studies on left AnG memory function (e.g., Yazar, Bergström, & Simons, 2014; 2017). However, the wide confidence intervals reported in many of the present analyses indicate a high degree of uncertainty in estimates, which may be attributable to the stimulation protocol used in this study. Moreover, the RT effects indicated in the main analyses were not significantly correlated with the intensity of stimulation,

although this may be due to low variability in the latter variable. In light of these caveats, the interpretation of cTBS effects on RT is done tentatively.

The selective left AnG cTBS modulation of multimodal versus unimodal episodic associative recognition and semantic relatedness RTs is consistent with a domain-general sensitivity to the sensory modality of information during declarative memory retrieval. This broadly agrees with previous neuroimaging evidence (Bonnici et al., 2016) and conceptually replicates the brain stimulation findings of Yazar, Bergström, & Simons (2017), who tested multimodal integration during episodic retrieval only. However, it should be cautioned that using the same testing materials in both retrieval tasks might have confounded episodic and semantic memory retrieval effects in the main RT analyses. As noted previously, the importance of AnG in semantic processing is controversial (Humphreys et al., 2017; 2022; Humphreys, Jung, & Lambon Ralph 2022; Humphreys & Tibon, 2023, Lambon Ralph et al., 2017). Thus, it is possible that the cTBS effect on semantic relatedness RT is instead related to incidental episodic memory retrieval. This may explain the relatively longer RTs observed in the former task. However, the stronger stimulation effect on semantic relatedness RT rather than associative recognition RT argues against this interpretation, as the latter should capture episodic retrieval processes more purely. Furthermore, exploratory analysis examining potential opposing stimulation effects on episodic and semantic memory retrieval found no significant differences. Critically, analysis of associative recognition task performance and confidence ratings suggested little contribution of recollection-based episodic memory retrieval, which the AnG is thought to support (see Hutchinson et al., 2009; Vilberg & Rugg, 2008; Wagner et al., 2005 for reviews). Nevertheless, future work testing domain-general accounts for AnG mnemonic function should endeavour to adequately separate episodic and semantic memory processes.

One way in which the apparently similar processing carried out by the AnG may differ from other integrative hubs is the nature of information operated on. It has long been held that semantic knowledge is represented at different levels of abstraction (Collins & Quillian, 1969; Rosch, 1978). If the ATL serves as a high-level amodal semantic hub (Patterson et al., 2007; Patterson & Lambon Ralph, 2016), then the AnG might act as a lower-level multimodal hub, facilitating the linking of sensory-perceptual representations with symbolic ones for conceptual elaboration (Kuhnke et al., 2023; Peelen & Caramazza, 2012; Reilly et al., 2016). With respect to episodic memory retrieval, integrative processing within the AnG may differ from that within the HPC in terms of its spatial framework. That is,

egocentric (i.e., self-referential) processes supported by the AnG (e.g., Ciaramelli et al., 2010b), possibly in coordination with other parietal regions such as the precuneus (Cavanna & Trimble, 2006), may mentally place the rememberer within previously experienced scenes, reconstructed from allocentric map-like representations supported by the HPC (Bird & Burgess, 2008; Burgess, Maguire, & O’Keefe, 2002). Indeed, recent brain stimulation (Bonnici et al., 2018) as well as functional neuroimaging and patient evidence (Russell et al., 2019) suggests a first-person visuospatial perspective may be critical to the subjective reliving of past experiences (Simons, Ritchey, & Fernyhough, 2022; Zaman & Russell, 2022).

Information buffering accounts such as the PUCC model (Humphreys & Lambon Ralph, 2015), which may provide a unifying explanation of episodic and semantic memory findings, have argued that, rather than integrating consolidated long-term stored multimodal representations (Shimamura, 2011), the key function of the AnG might instead be the temporary online buffering of multisensory spatiotemporally extended representations (Humphreys, Jackson, Lambon Ralph, 2020; Humphreys, Lambon Ralph, & Simons, 2021; Humphreys & Tibon, 2022; Humphreys et al., 2022). The present findings are compatible with the PUCC model given that left AnG stimulation was found to modulate RTs during episodic and semantic memory retrieval of stimuli presented over an extended time window (i.e., pair associates studied and tested sequentially over the span of several seconds). This is also consistent with previous fMRI and TMS findings implicating the region in time-extended information integration during narrative reading (Branzi et al., 2020; 2021) and evidence that temporoparietal lesions in semantic aphasia patients impairs the ability to flexibly use and manipulate information (Jefferies & Lambon Ralph, 2006), which presumably would require a multimodal spatiotemporal information buffer.

While the facilitatory stimulation effect observed on RT in the current study was unexpected given the traditionally assumed inhibitory effect of cTBS, such discrepancies are not unheard of in non-invasive brain stimulation studies. For example, Bonni et al. (2015) found cTBS applied to the left precuneus of the medial parietal cortex, which resulted in improved contextual retrieval as evidenced by a selective decrease in memory errors. Wynn et al. (2018) delivered conventionally inhibitory 1Hz repetitive TMS to the left AnG and found recollection to be unaffected whereas both familiarity and subjective memory confidence were improved in low baseline performance participants. Recent evidence suggests the direction stimulation effects on memory processes may depend on brain-state at

the time of stimulation (e.g., Ezzyat et al., 2017), with stimulation decreasing memory performance only when it is delivered during optimal states (Hanslmayr & Roux, 2017). Considering this, it is possible that the reading and perceptual copy tasks participants performed during the break period of the present study (during which cTBS was administered) might have had the unintended consequence of enhancing subsequent declarative memory retrieval. Additionally, the high mean baseline level of associative recognition performance in the present study compared to others employing more challenging source memory tasks (e.g., Yazar, Bergström, & Simons, 2017), may explain why the same facilitatory cTBS effects were not found on objective and subjective associative recognition performance measures.

Given increasing evidence for substantial intra- and interindividual variability in susceptibility to theta burst stimulation (Corp et al., 2020; Jannati et al., 2017; Lowe & Hall, 2018), the stimulation protocol used in this study might have contributed to the lack of stimulation effects on non-RT measures in the associative recognition task. Moreover, although shorter trains such as the one employed in here are typical in cTBS studies, longer trains may be more consistent in eliciting neurophysiological effects as determined by motor evoked potentials (McCalley et al., 2021; but see Gamboa et al., 2010). Such interindividual variability might therefore have obscured true but divergent stimulation effects on the objective and subjective associative recognition measures, the possibility of which was explored by re-analysing participants according to the direction of their RT effect. No significant selective AnG stimulation effects were found in either subgroup. Likewise, more granular trial-level analysis accounting for interindividual variability in the stimulation effect did not uncover any significant differences either. However, these exploratory analyses were most likely underpowered. Therefore, future theta burst stimulation studies may instead benefit from a multi-level modelling approach to analysis, which can statistically account for variability in response to brain stimulation at the subject level.

The absence of AnG cTBS effects on objective associative recognition performance may be attributable to the memory task itself. In the present study, participants were tested on sequentially presented colour line drawings of objects and/or sounds associated with objects. In comparison, others have used time-extended audio-visual clips (Bonnici et al., 2016) or concurrently presented object-in-scene photographs and spoken object names (Yazar, Bergström, & Simons, 2017) to investigate AnG involvement in multimodal episodic retrieval. Thus, the stimuli used here lacked a spatial context, which might be an essential element of episodic memory representations (Herwig et al., 2020; Robin, Buchsbaum, &

Moscovitch, 2018). If the left AnG enables the subjective re-experiencing of past events through holistic memory retrieval (Simons, Ritchey, & Fernyhough, 2022), then it is possible that retrieval of multimodal stimuli alone may not be sufficient to recruit the region. However, hippocampal-targeted high-frequency repeated TMS of posterior parietal cortex, repeated over several days before test, has previously been shown to enhance subsequent cued recall of multimodal face-word associations (Wang et al., 2014). Moreover, a large sample of (predominantly right-hemisphere) parietal lesion patients ($n = 60$) exhibited the greatest cued recall deficits for multimodal object picture-sound pairs and not unimodal object picture or sound pairs (Ben-Zvi, Soroker, & Levy, 2015; but see Berryhill, Drowos, & Olson, 2009, whose patients had normal associative recognition accuracy for audio-visual pairs but reduced confidence). Lesion-symptom mapping in these same patients implicated the AnG specifically multimodal associative recognition impairments.

While associative recognition is thought to rely primarily on recollection (Donaldson & Rugg, 1998; Hockley & Consoli, 1999; Yonelinas, 1997), its relative contribution can diminish in favour of acontextual familiarity when associates are unitized during encoding (Graf & Schacter, 1989), thus bypassing the need for contextual episodic retrieval. This possibility is supported by the shape of ROC curves derived from the present data, which indicate largely familiarity-based episodic recall. Moreover, the AnG is associated with recollection whereas more dorsal lateral parietal cortex is associated with familiarity (for reviews, see Hutchinson et al., 2009; Vilberg & Rugg, 2008; Wagner et al., 2005). Thus, AnG involvement may not have been necessary for successful episodic memory task performance in this study. Nevertheless, several aspects of the current associative recognition task should have discouraged unitization. First, no unstudied objects were tested. Therefore, the intact and rearranged pairs, the latter of which were created by simply recombining different studied pairs, should have had similar levels of familiarity. Second, the sequential rather than concurrent presentation of objects in each study pair should have made perceptual unitization more challenging (Parks & Yonelinas, 2015). However, it should be noted that unitization can operate at an abstract level (Li et al., 2019). Finally, the relative size encoding task should have emphasized the differences between objects in each pair rather than their similarities, similarly discouraging unitisation (Opitz & Cornell, 2006). Admittedly, however, it is possible that the 10s response deadline for these judgements was too generous, thus permitting reliance on alternative strategies that promote more holistic processing fostering unitization (e.g., visualising the objects together in scenes or forming short narratives).

Finally, the lack of AnG cTBS modulation of subjective confidence in the associative recognition memory judgements is intriguing given the proposed role of the region in the subjective experience of remembering (Simons, Ritchey, & Fernyhough, 2022). For example, AnG cTBS in neurologically healthy younger adults has previously been shown to reduce confidence in source memory judgements and not in simple item recognition or cued recall judgements (Yazar, Bergström, & Simons, 2014), which is similarly corroborated by parietal patient data (Simons et al., 2010). More recent work suggests the AnG may not be directly involved in memory confidence judgements. Rather, the AnG might promote mnemonic metacognition by gauging the subjective vividness (Zou & Kwok, 2022; but see Ye et al., 2018, who implicate the precuneus) of the high fidelity representations it supports (Richter et al., 2016). However, functional neuroimaging has implicated the precuneus in episodic memory-related mental imagery (see Cavanna & Trimble, 2006 for review), and Sreekumar et al. (2018) related multivoxel patterns of activity within the right precuneus to detailed subjective content representations during autobiographical recollection, indicating that different PPC regions might work together to gauge subjective vividness. Thus, further work is needed to delineate the specific contributions of the AnG and precuneus in this regard. Moreover, it is possible that associative recognition tasks such as the present one do not facilitate the formation of particularly high fidelity or vivid representations, which may therefore not require metacognitive processes supported these PPC regions.

To conclude, the experiment reported in this chapter investigated whether the left AnG is necessary for integrating multimodal information during episodic and semantic memory retrieval. This hypothesis was tested by examining the effects of left AnG cTBS, relative to vertex control stimulation, on episodic associative recognition and semantic relatedness retrieval tasks involving unimodal and multimodal associates. Left AnG cTBS was found to selective modulate RT in both retrieval tasks, proving some of the first causal brain stimulation evidence for a domain-general integrative role for the region during different forms of declarative memory retrieval. However, this stimulation effect was unexpectedly facilitatory, and no additional stimulation effects were found on objective or subjective associative recognition performance measures. Further research is needed to explore the nature of information processing operations carried out within the left AnG during declarative memory retrieval, which may differ by subregion (Nelson et al., 2010; Nelson et al., 2013), as well its interactions with other integration hubs.

Chapter 3: First-Person Recall and its Neuroanatomical Correlates in Normal Ageing

This study originally aimed to test the causal role of the left AnG in first-person episodic recall using non-invasive brain stimulation in healthy younger adults. For this purpose, I developed a custom 3D object location memory task that varies both encoding and retrieval perspective, as well as a custom trial-locked online repetitive transcranial magnetic stimulation procedure. However, the COVID-19 pandemic intervened before this version of the study could be realised. Instead, I adapted my research question to investigate first-person episodic recall in normal ageing, developing an online version of the object location memory task that could be administered to both healthy younger and older adults via the internet. As the older adult participants had previously been scanned using MRI, I additionally used voxel-based morphometry to identify the parietal neuroanatomical correlates of first-person recall in the elderly. The results from this study support a general age-related deficit in first-person recall, regardless of the original encoding perspective. A less pronounced but more specific age impairment was also found for third-person recall when object locations were encoded from the same perspective and not a first person one. Furthermore, I found grey matter volume within the left angular gyrus (and to a lesser extent, the precuneus) to positively correlate with the adoption of a first-person perspective during recall. No such association was found with first-person recall more generally, however. Both left angular gyrus and precuneus volumes were shown to decline with age. These findings illustrate objective age differences in first-person recall and identify the left angular gyrus as a possible neural substrate for the adoption of this recall perspective more specifically.

Introduction

Different visuospatial perspectives can be adopted during episodic recall, which can shape recollective experience (Nigro & Neisser, 1983). For example, recalling personal events from an own-eyes or “field” (i.e., first-person) perspective tends to evoke the sensory and internal details of that event including associated feelings, sensations, and thoughts (Berntsen & Rubin, 2006; McIsaac & Eich, 2002; Robinson & Swanson, 1993; Sutin & Robins, 2010). In contrast, events recalled from an external or “observer” (i.e., third-person) vantage point are often lacking in perceptual imagery, rated as less self-relevant, contain more spatial information, and are possibly more semantic in nature (Berntsen & Rubin, 2006; Brewer, 1996; Frank & Gilovich, 1989; McIsaac & Eich, 2002; Mooren et al., 2016). Critically, subjective ratings of memory vividness have been correlated with first-person perspective autobiographical memory (ABM) recall (Rice & Rubin, 2011). Considering these phenomenological differences, a first-person visual perspective has been proposed as an integral factor in enabling the subjective re-living of past experiences through episodic memory (Simons, Ritchey, & Fernyhough, 2022), as well as in broader autonoetic consciousness (Zaman & Russell, 2022) and self-consciousness (Vogele et al., 2004).

While personal events are typically experienced and recalled from a first-person perspective, there are many exceptions. For example, highly stressful or emotionally negative (McCarroll, 2017), even traumatic (McIsaac & Eich, 2004), events can also be experienced and recalled from a third-person observer perspective, possibly as a psychological distancing mechanism. False memories (Heaps & Nash, 2001) and memories that conflict with one’s current self-beliefs (Libby & Eibach, 2002) are also often visualised from a third-person perspective. Additionally, memories from childhood are associated more with a third-person observer perspective than memories formed during adulthood (Lorenz & Neisser, 1985). The visual perspective of episodic recall changes even as memories themselves age, with remote memories more prone to being remembered from a third-person perspective than recent ones (McIsaac & Eich, 2002; Rice & Rubin, 2009; Robinson & Swanson, 1993). Recall perspective can also be experimentally manipulated. For example, Marcotti & St. Jacques (2022) recently showed that reviewing photographs of events experienced in first person, but presented from a third-person perspective, promotes the adoption of an observer perspective when remembering those events. In immersive virtual reality tasks, third-person perspective experiences during encoding have also been demonstrated to create third-person memories as indicated by increased ratings of observer-like perspectives during remembering (Iriye & St.

Jacques, 2021). Relatedly, perceptual out-of-body illusions induced by synchronous visuotactile stimulation during simulated social interactions leads to reduced delayed recall from a first-person perspective relative to recall of interactions encoded in an in-body control condition (Bergouignan, Nyberg, & Ehrsson, 2022).

Evidence from patients suggests overlapping regions of the parietal cortex may be critical for the conscious sense of embodied self-location from a first-person perspective (for review see Ionta, Gassert, & Blanke, 2011) and episodic memory (Bréchet et al., 2018). Out-of-body experiences, a form of autoscopic phenomena characterised by hallucinatory disembodied visual perspectives, can be induced either spontaneously in epileptic patients with seizures originating around the temporo-parietal junction (Hoepner et al., 2015) and in neurological patients with damage localised to the same area (Blanke et al., 2004), or intentionally in epileptic patients using focal electrical stimulation of the AnG (Blanke et al., 2002). Patients with left- or right-hemisphere posterior parietal cortex damage exhibit deficits in egocentric (i.e., self-referential) spatial navigation ability as well as impoverished and disembodied re-experiencing in remote spatial memory tasks (Ciaramelli et al., 2010b). In perspective shifting tasks, right-hemisphere parietal patients with lesions encompassing the angular gyrus (AnG) of the inferior parietal lobule are impaired at judging whether scenes were studied from their own first-person perspective or an alternative observer viewpoint, despite normal item location and recognition memory (Russell et al., 2019).

In neuroimaging studies of neurologically healthy younger adults (YAs), left AnG involvement has frequently been observed during detailed recollection (for reviews, see Vilberg & Rugg, 2008; Rugg & King, 2017; Rugg & Vilberg, 2013). Functional magnetic resonance imaging (fMRI) indicates the region is preferentially engaged during the retrieval of multimodal audio-visual versus unimodal audio or visual episodic memories (Bonnici et al., 2016; Tibon et al., 2019). Additionally, individual multimodal episodic memories have been decoded from activity patterns within the left AnG using multivoxel pattern analysis, the classification accuracy of which tracked subjective memory vividness (Bonnici et al., 2016). Non-invasive brain stimulation techniques producing temporary “virtual lesions” in targeted brain regions have also been used to establish the AnG’s causal role in episodic memory recall. Continuous theta burst stimulation (cTBS) of the left AnG has been shown to cause a selective reduction in source memory confidence ratings while leaving performance in various episodic memory tasks unaffected (Yazar, Bergström, & Simons, 2014). Left AnG stimulation under the same protocol has further been shown to disrupt the retrieval of

multimodal but not unimodal episodic memories in 2D scene memory task (Yazar, Bergström, & Simons, 2017). As in parietal epilepsy patients (Blanke et al., 2002), anodal versus sham high-definition transcranial direct current stimulation of the right AnG in healthy YAs can result in out-of-body illusions as well as reduce the ability to discriminate self from other perspectives (Boer et al., 2020). Left AnG cTBS has also recently been shown to disrupt the relationship between memory fidelity and the ability to distinguish perceived from imagined self-initiated actions, but not those initiated by another agent, in a reality monitoring task (Kwon et al., 2022). Finally, repetitive transcranial magnetic stimulation of the left AnG has been found to reduce the number of internal details produced during episodic simulation and first-person ABM recall tasks (Thakral, Madore, & Schacter, 2017), and cTBS thereof decreases the tendency to report experiencing a first-person perspective during ABM recall (Bonnici et al., 2018). Such findings have led to the proposal that the left AnG is necessary for integrating multimodal memory representations within an egocentric framework during recollection (Simons, Ritchey, & Fernyhough, 2022).

The precuneus of the medial superior parietal lobule has, like the AnG, been implicated in various processes related to recollection in healthy YAs (for review, see Cavanna & Trimble, 2006). In an influential early positron emission tomography study, activity in the precuneus was associated with memory-related imagery (Fletcher et al., 1995). In more recent fMRI studies, precuneus activity has been observed in change detection tasks during mental viewpoint and object array rotation (Lambrey et al., 2012) and when novel visual perspectives are adopted during ABM recall (Faul et al., 2020). Moreover, fMRI activity in the precuneus has been tied to first-person perspective taking (Ruby & Decety, 2001; Vogeley & Fink, 2003), and its grey matter volume (GMV) has been associated with the propensity for first-person ABM recall (Freton et al., 2014; Hebscher, Levine, & Gilboa, 2018). Like the AnG (Bonnici et al., 2016), activity within the precuneus has been shown to track the subjective vividness of recall in complex episodic memory tasks (Richter et al., 2016), and representations of memory contents have likewise been decoded from activity patterns within the region during vivid versus non-vivid ABM recall (Sreekumar et al., 2018). In combined cTBS and magnetoencephalography studies, left precuneus stimulation has been shown to modulate oscillatory activity associated with complex memory retrieval and a parietal signature of ABM perspective ratings (Hebscher, Meltzer, & Gilboa, 2019), but not perspective ratings themselves (Hebscher, Ibrahim, & Gilboa, 2020). Recently, activity within both the precuneus and AnG has been associated with shifting from a first-person

own-eyes to a third-person observer perspective during recall (Iriye & St. Jacques, 2018; Marcotti & St. Jacques, 2018; St. Jacques, Szpunar, & Schacter, 2017), suggesting each parietal region makes potentially subtly different contributions to first-person recollection.

Memory difficulties are commonly reported by the elderly (Steinberg et al., 2013) and often presage future cognitive impairment (Begum et al., 2012; Jonker, Geerlings, & Schmand, 2000; Mogle, Hill, & McDermott, 2017; Reid & MacLullich, 2006). Even in normal ageing, memory complaints frequently accompany behavioural and phenomenological changes in remembering. For example, older adults (OAs) report fewer internal details relative to external ones when recalling events from their lives (Gaesser et al., 2011). Compared against YAs, OAs have also reported an increased tendency to experience recent ABMs from a third-person “observer” perspective rather than a first-person “field” perspective (Piolino et al., 2006; 2009). In the same studies, Piolino et al. additionally probed the subjective experience of ABM recall using the remember/know procedure, where “remember” and “know” responses can be taken as proxies for the level of subjective re-experiencing. During recent ABM recall, OAs were found to give more “know” than “remember” responses, indicating diminished recollective richness (see also St. Jacques & Levine, 2007). However, not all studies of ABM have found age differences in recall perspective, both when the age of the memories is accounted for (Kapsetaki et al., 2022) and when it is not (Rathbone et al., 2015). OAs also somewhat paradoxically tend to report equivalent or greater levels of subjective memory vividness in standard lab-based memory tasks despite poorer objective memory performance when compared against YAs (e.g., retrieving fewer episodic details). This dissociation has been taken as evidence for age differences in gauging memory vividness (for review, see Folville et al., 2021) and linked to reduced precuneus activity in OAs relative to YAs (Folville et al., 2020). The mixed findings from subjective ABM reports in particular highlight the need for more objective measures of visual perspective in OAs, especially when potential age-related deficits in first-person recall are likely to be more subtle than those indicated in parietal patients.

Different visual perspectives are associated with the adoption of certain spatial frames of reference, which change the relationship between an individual and their environment. A first-person, ground-level point of view has been shown to facilitate object-to-self (i.e., egocentric) spatial relations whereas a third-person, aerial viewpoint encourages object-to-object (i.e., allocentric) relations (Torok et al., 2014). As with a first-person visual perspective, an egocentric spatial framework centred on one’s body is typically favoured,

although reference frames can be flexibly switched or combined when necessary (Burgess, 2006; Ekstrom, Arnold, & Laira, 2014; Rice & Rubin, 2011). While this egocentric preference appears to be mostly intact for spatial navigation in the elderly, the existence of age-related egocentric spatial memory deficits is less clear (for review, see Colombo et al., 2017). Such deficits have been found in OAs when egocentric spatial memory is tested exclusively (Korman et al., 2019; Pouliot & Gagnon, 2005) or sometimes alongside allocentric impairments (Fernandez-Baizan, 2019; Fernandez-Baizan, Arias, & Mendez, 2020; Lopez et al., 2019; Merriman et al., 2016; Merriman et al., 2018; Yamamoto & DeGirolamo, 2012). Moreover, large sample studies investigating both egocentric and allocentric spatial memory abilities across the lifespan have found comparatively greater decline in egocentric memory ability in adults aged 60 years or older (Iachini, Ruggiero, & Ruotolo, 2009; Ruggiero, D'Errico, & Iachini, 2016). Similar to observations by Piolino et al. regarding ABM (2006; 2009), fewer OAs than YAs have reported imagining learned routes from a first-person perspective and in less perceptually detail with a reduced sense of re-experiencing (Rosenbaum et al., 2012). However, there is currently a dearth of studies comparing memory abilities of the elderly across different spatial reference frames.

More recently, spatial memory tasks have been leveraged to directly examine age effects on egocentric/first-person recall. Using a novel in-person 3D scene memory task, Russell et al. (2019) showed that healthy OAs were less able than YAs to discriminate whether tested scenes composed of object arrays were encoded from their own first-person perspective or shifted to a third-person observer perspective, despite normal item recognition and location memory. In the same study, the authors found bilateral activity in ventral parietal regions including the AnG to be sensitive to such perspective shift judgements in OAs. The behavioural finding by Russell et al. that OAs are less able to identify their own encoding perspective was conceptually replicated in a follow-up study Kapsetaki et al. (2022), who used a similar 3D scene memory task. However, the OAs in Kapsetaki et al.'s study did not differ from YAs when additionally interviewed about the visual perspective of their recollective experience, although the authors speculated that this may be attributable to the manner of questioning. Ladyka-Wojcik et al. (2021) used an immersive 3D virtual reality object location memory task to investigate the behavioural effects of switching bi-directionally between egocentric and allocentric spatial reference frames in normal ageing by manipulating visual perspective. They found OAs recalled object locations less accurately when tested in a first-person perspective versus a third-person perspective. Furthermore, a

directional switch cost was discovered for third-person recall of object locations that were learned egocentrically, in a first-person perspective. No YA comparison group was included in this study, however. While suggestive, it is presently unclear from this evidence whether first-person recall or more general perspective switching ability is affected in normal ageing.

The study presented in this chapter tested whether first-person perspective episodic recall, which may play an important role in facilitating subjective memory reliving (Simons, Ritchey, & Fernyhough, 2022; Zaman & Russell, 2022), is impaired with age. To this end, a mixed design was employed in which healthy YA and OA age groups completed a custom 3D object location memory task. In this task, participants studied object locations in familiar virtual environments from either a first-person or third-person perspective. Critically, the perspective from which these object locations were subsequently recalled during test varied between the same and alternative studied perspectives. This resulted in four task conditions: stay first person (i.e., studied and tested in a first-person perspective), switch first person (i.e., studied in third person but tested in first person), stay third person (i.e., studied and tested in a third-person perspective), and switch third person (i.e., studied in first person but tested in third person).

Based on evidence from healthy YAs indicating that third-person remembering benefits spatial memory accuracy (Iriye & St. Jacques, 2021), first-person recall of object locations was predicted to be comparatively less accurate and have longer response times (RTs) in both YAs and OAs. Switching visual perspective between study and test phases was expected to lead to lower recall accuracy and slower RTs than when the perspective remained unchanged (Marcotti & St. Jacques, 2018). As perspective switching might place greater demands on cognitive control abilities (Bradford, Jentsch, & Gomez, 2015; Qureshi, Apperly, & Samson, 2010; but see also Qureshi & Monk, 2018), which are thought to decline with age due to structural and functional changes in the prefrontal cortex (Braver & Barch, 2002; Paxton et al., 2008; Raja & D'Esposito, 2005), OAs were predicted to show a greater switch cost relative to YAs. Finally, OAs were predicted to have worse overall performance and longer RTs than YAs, consistent with general age-related memory decline and cognitive slowing (Hedden & Gabrieli, 2004).

Three possible hypotheses regarding the roles of the left AnG and precuneus in the visual perspective of recall were investigated in OAs using voxel-based morphometry (VBM), an automated technique that allows voxelwise analysis of GMV (Ashburner & Friston, 2000). It was predicted that if either of these regions support the general ability to

adopt alternative visual perspectives, then a positive correlation between its GMV and switch trial performance, irrespective of the test perspective, should be observed. If, instead, the left AnG or precuneus supports the specific adoption of a first-person perspective, then a positive correlation is predicted between its GMV and switch trial performance when the test perspective is first person. However, if either region supports first-person memory representation more directly, then its GMV should positively correlate with performance on trials in which object locations were both studied and tested in a first-person perspective. Based on observations of higher-than-average age-related atrophy in the parietal lobes (Fjell et al., 2009; Habes et al., 2016; Raz et al., 2004; Resnick et al., 2003; Salat et al., 2004), OAs were additionally predicted to have lower parietal GMV when compared against YAs.

Materials and Methods

Participants

Older adults. 27 OAs (56% male) aged 65 – 84 years ($M = 74.37$, $SD = 4.72$) whose mean level of formal education was 17 years ($SD = 5.20$, range = 8 – 34) were included in all analyses. Structural MRI (sMRI) scans (and neuropsychological measures) were previously acquired for all OAs as part of an unrelated study, 2.39 – 4.90 years ($M = 3.92$, $SD = 1.03$) before participation in the present study. All OAs tested in the present study were screened before scanning for cognitive decline beyond that which is expected in normal ageing (Petersen et al., 1999) using the Montreal Cognitive Screening Assessment (MoCA; Nasreddine et al., 2005). These participants had MoCA scores within the normal range of 26 – 30 ($M = 27.70$, $SD = 1.35$). During the same period, the Trail Making Test (Tombaugh, 2004) and a custom recognition memory test were also administered to measure respective general executive and memory abilities. These measures are reported here as the difference in completion time (in seconds) between parts B and A of the Trail Making Test (Sanchez-Cubillo et al., 2009) and the standardised response bias-corrected recognition score (as in the previous chapter). A further 16 OAs were tested in the present study but excluded due to MoCA scores indicating mild cognitive impairment ($MoCA < 26$), below chance-level performance on the main task, withdrawal from the study, or technical issues.

Younger adults. 17 YAs (53% male) aged 18 – 33 years ($M = 24.12$, $SD = 4.27$) whose mean formal education level was 18.06 years ($SD = 1.95$, range = 15 – 21) were included in the behavioural analysis of memory performance. One participant, however, was excluded from the analysis of RTs due to a suspected technical issue affecting measurement accuracy. An additional YA was tested but excluded for not completing the study. In contrast

to the OAs, sMRI scans were only available for 8 YAs. These participants were scanned 2.17 – 4.26 years ($M = 3.03$, $SD = 0.59$) prior to testing. The remaining 9 YAs without scans participated in the final behavioural pilot study for the object location memory task, which was identical to the version presented here. Unlike the OAs, no cognitive measures were available for any of the YAs.

All participants in both age groups were right-handed native English speakers with normal or corrected-to-normal vision. No participants reported current or historical diagnoses of developmental, psychiatric, or neurological conditions at the time of testing. The OAs were members of local church and community groups in Cambridge including the University of the Third Age, whereas the YAs were students at Cambridge University. Due to pandemic-related restrictions precluding the acquisition of more current MRI and cognitive data, all participants were recruited from research volunteer databases maintained by the Cambridge Memory Laboratory and the MRC Cognition and Brain Sciences Unit participant panel. This limited the pool of eligible participants and prevented the matching of age group sample sizes. All participants gave informed consent before commencing the study and were remunerated in a manner approved by the University of Cambridge Human Biology Research Ethics Committee.

Stimuli

Stimuli consisted of 80 target and 40 landmark object images in the main task. Targets were unique 256 x 256 pixel colour images of common objects. Landmarks were images of distinctive natural and artificial environmental features 512 pixels high, with varying widths ($M = 526$, $SD = 244.8$, range = 167 – 1134). Both targets and landmarks were rendered as view plane-aligned 2D sprites so that the same object face was always shown, which ensured the same object information was presented in first-person and third-person viewpoints (see Figure 1 for example stimuli). In the testing environment, targets had a true height and width of 1.25 virtual meters (vm) whereas landmarks were 2.5vm tall. Stimuli were obtained from various internet sources and processed using Paint.NET (v4.3.2; Brewster, 2021) and custom MATLAB scripts (v2021b; The MathWorks, 2021).

Testing environment

Participants were tested within a 3D virtual circular environment 50vm in diameter with a solid light grey floor and bounded by a 4vm high solid dark grey wall (see Figure 2). These dimensions were comparable to those employed in similar object location memory tasks (e.g., Bellmund et al., 2020). Four equally spaced distal landmarks were placed 5vm

beyond the boundary wall, with one situated at each cardinal direction (i.e., North, South, East, and West). Landmark sets persisted for the duration of each testing block, serving as both locational memory aids and stable orientation cues. The sky, which was visible only in the first-person perspective, had a naturalistic blue gradient but was featureless. Participants viewed the environment in a standard 16:9 aspect ratio. The first-person camera had a fixed 60° field of view (FOV), was oriented perpendicular to the ground, and was placed 1.5vm high to approximate the height of an average person. In contrast, the third-person camera had a variable FOV (10 – 75°), was angled 90° down toward the ground, and had a fixed height of 55vm. The virtual environment was created using the Unity game engine (v2019.4.19f1; Epic Games, 2019).

Movement and camera controls

In both perspectives, participants pressed the ‘a’, ‘d’, ‘w’, and ‘s’ keyboard keys to move left, right, forward, and backward with an acceleration of 0.3vm/second (s) and a maximum speed of 25vm/s. This permitted quick traversal of the environment while simultaneously allowing fine positional adjustments within the span of a trial. When in the first-person view, participants could move their computer mouse to laterally rotate the camera and their heading at 200 arbitrary units/s. In the third-person view, moving the computer mouse adjusted camera FOV at 40 units/s, enabling closer inspection of target and landmark objects. All rates of change were multiplied by the interval (in s) between the previous and current frames to ensure consistency across devices. These movement and camera controls were used in all phases of the object location memory task, except for the arithmetic phase.

Procedure

In a mixed design, the YA and OA groups completed a custom computer-based 3D object location memory task in which visual perspective was manipulated within subjects during both encoding and retrieval. Testing was completed online in a single session involving one practice block followed by 10 testing blocks. All blocks consisted of exploration, study, arithmetic, and test phases (see Figure 1 for a schematic representation of the task). Briefly, the exploration phase allowed participants to familiarise themselves with the virtual testing environment, which changed each block. During the study phase, participants sequentially learned the location of several target objects relative to distal landmarks and from either a first-person or third-person perspective. To discourage memory rehearsal between study and test phases, participants solved simple arithmetic problems during the arithmetic phase. In the test phase, participants reported the location of target

objects from a perspective that either matched or opposed the studied one (see Appendix for the full task instructions shown to participants). Participants completed a total of 80 test trials in the main task, which were equally divided across the 10 testing blocks (i.e., 8 target object locations were tested per block) and the four task conditions (i.e., 20 target object locations were tested in stay first person trials, 20 in switch first person trials, 20 in stay third person trials, and 20 in switch third person trials). A series of pilot studies were conducted to find the optimal combination of target set size, landmark number, trial duration, and environment size. The task was coded in C# and JavaScript, hosted on a private GitHub Page site, and run in-browser using WebGL. Data were anonymously collected using a secure Google FireBase realtime database.

First, participants began the exploration phase at the centre of the testing environment with no target objects present, viewing it from either a first-person or third-person perspective (see Figure 1 for example). After 15s elapsed, participants were placed once again at the centre of the environment and viewed it for another 15s from the alternative perspective. Initially, the first-person camera faced a random direction whereas the third-person camera was placed at a height of 55vm with a 75° FOV so that all distal landmarks were fully visible. Using the controls described in the previous section, participants could freely explore the environment in both perspectives for greater immersion and to gain familiarity with the landmarks, which were randomly selected and changed every block.

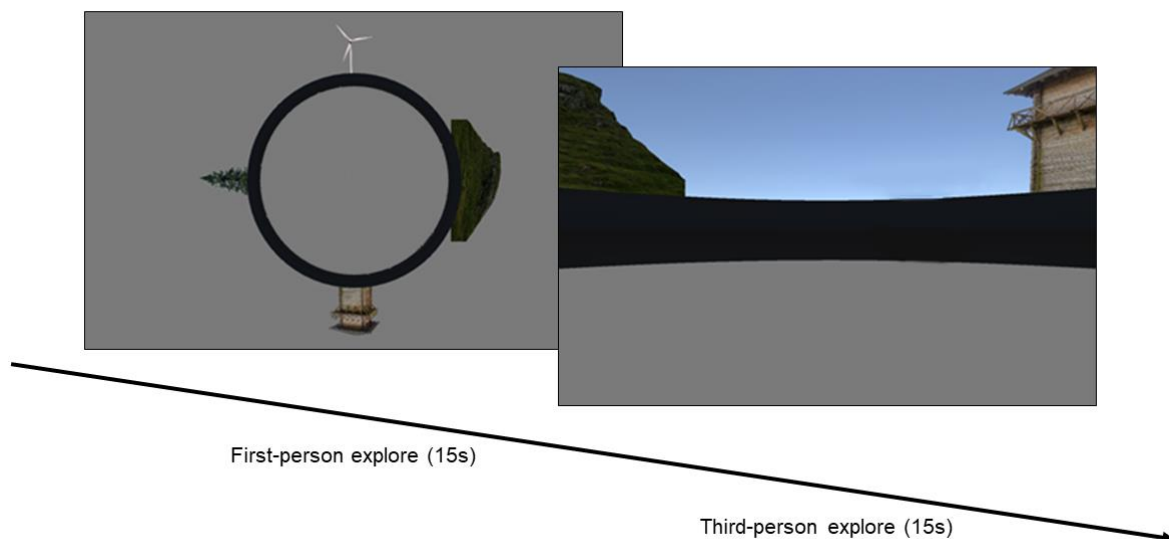


Figure 1. Exploration phase of the object location memory task. In this first phase of a testing block, participants initially familiarised themselves with the testing environment from third-person and first-person perspectives. Note that these perspectives were shown in a random order within each block.

Next, in the study phase, participants memorised eight target object locations relative to the landmarks (see Figure 2). Targets were uniformly randomly distributed within the environment but were constrained to within a 20vm radius to prevent occlusion by the boundary wall. The location of each target was memorised sequentially, yielding eight study trials per block. Study trials began with a central black fixation cross presented for 500ms against a grey background, followed by a fixed 10s period in which participants memorised a target location. Participants began this period at the centre of the environment, which they viewed from either a first-person or third-person perspective. The studied perspective randomly varied across trials and in equal proportion. Furthermore, the first-person camera initially faced the target whereas the third-person camera was placed 55vm above the centre of the environment. This equated the maximum amount of time available to study a target location in both perspectives.

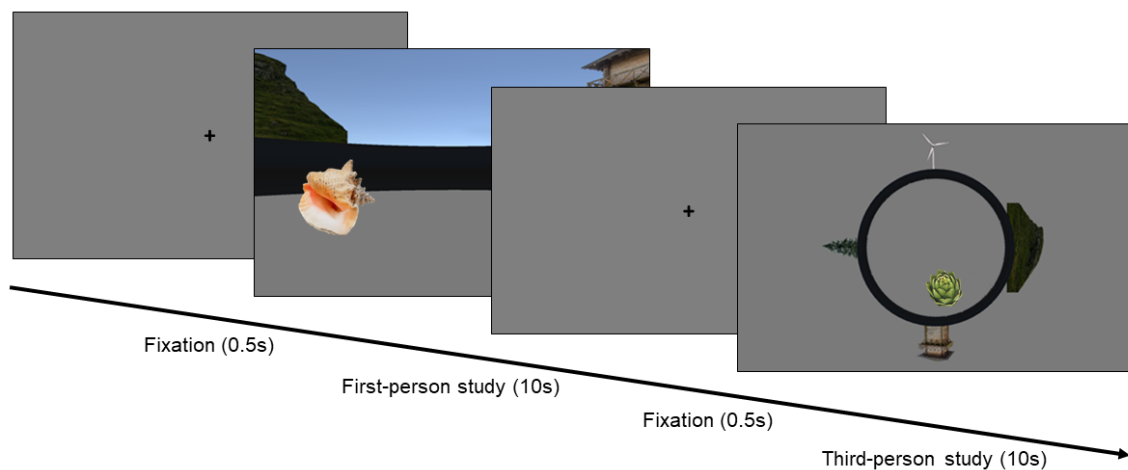


Figure 2. Study phase of the object location memory task. Here, participants sequentially learned the random locations of eight target objects from either a first-person or third-person perspective.

After memorising the target locations, participants completed the arithmetic phase, which served as both a distractor task and attention check (see Figure 3). The arithmetic phase lasted for 30s and involved solving simple addition and subtraction problems on positive double-digit integers. Arithmetic trials were self-paced and began with a 500ms central black fixation cross, followed by a randomly generated problem. Participants typed their answer, which was displayed on-screen, using the number keys on their keyboard. Mistakes could be deleted by pressing the ‘backspace’ key. Responses were submitted by pressing the ‘space’ key.

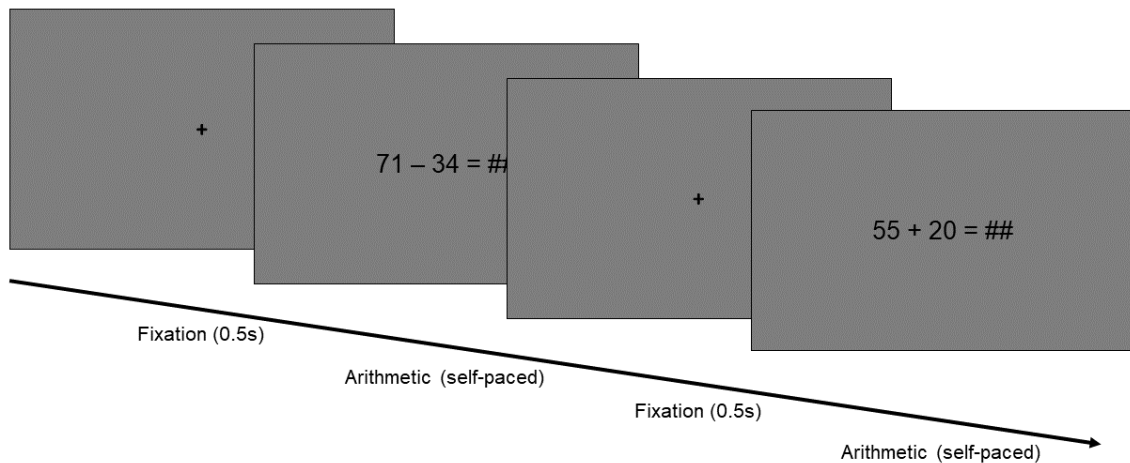


Figure 3. Arithmetic phase of the object location memory task. In this phase, participants were discouraged from rehearsing target object locations in working memory by completing simple addition and subtraction problems at their own pace.

Finally, in the test phase, participants were instructed to reproduce the studied target locations from memory as precisely as possible (see Figure 4). No new targets were presented, resulting in eight test trials per block. Test trials started with a 500ms central black fixation cross presented against a grey background, then recall was cued with the presentation of a target object for 1s. Following the cue, participants were placed at the centre of the environment in which they had to give a response. YAs had up to 15s to respond before trial timeout whereas OAs responded at their own pace. The response deadline was removed for OAs to reduce confounding age differences in the ability to report memory with memory performance. During the response period, participants moved a black crosshair to a remembered target location and pressed ‘space’ to submit their response. The crosshair, which facilitated precise indication of remembered target locations, was placed 6.75vm ahead of the first-person camera whereas the third-person camera was centred above it. As in previous phases, the third-person camera was initially placed at a height of 55vm. In contrast, the first-person camera initially faced a random direction. Targets were tested in a random order and the perspective randomly varied between studied and alternative perspectives (i.e., stay and switch trials, respectively).

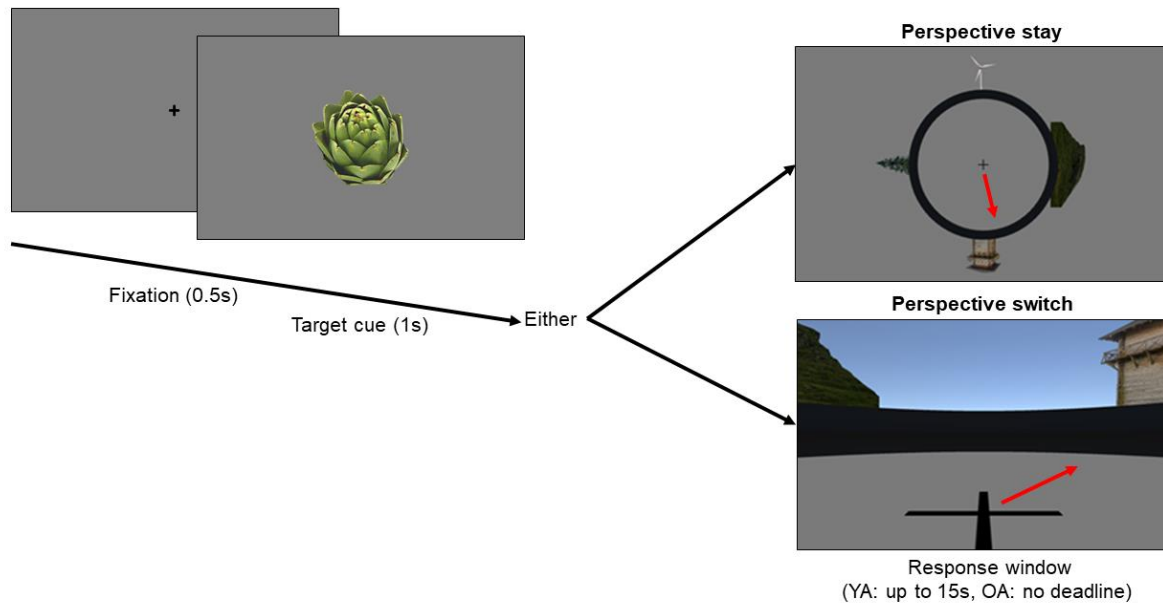


Figure 4. Test phase of the object location memory task. In this final phase, participants had to precisely move the crosshair to the studied location of each target object, initially cued with the object itself, from either the same study perspective (perspective stay condition) or alternative perspective (perspective switch condition). Red lines indicate where a participant should move the crosshair to indicate the example target object's true studied location. Note that all studied target object locations were tested, although the test perspective could be switched irrespective of the original study perspective, and that OAs had no response deadline.

Behavioural measures and analysis

Performance in the object location memory task was analysed using mean memory score (MS), derived from raw distance errors, and median RT (in s) measures. Distance error was quantified as the Euclidean distance (in vm) between target and response locations. However, as targets studied closer to an environment's boundary have a larger maximum possible distance error than those studied in its centre, a correction is needed to account for varying difficulty across different target locations. This was achieved by computing the accuracy percentile of a given response relative to all other possible responses as a MS (Jacobs et al., 2016). MSs were computed by first generating 10,000 possible response locations uniformly distributed throughout the environment. Next, the distance between each possible response location and a given target location was calculated, yielding trial-specific error distributions. Finally, the proportion of possible response errors less than the actual response error was calculated for each target, resulting in a MS ranging from 0 to 1. A MS of 1 corresponds to perfect performance, a score of 0.5 to chance level performance, and a score 0 to the worst possible performance (i.e., the furthest possible location from a true target

location). Trials in which participants gave no response or responded faster than 500ms were discarded (4% and 2% of all trials for YAs and OAs, respectively).

All behavioural analyses were conducted using R Statistical Software (v4.1.1; R Foundation for Statistical Computing, Vienna, Austria). Given the imbalance between YA and OA sample sizes, linear mixed models (LMMs) were run on mean MS and median RT using the ‘lme4’ package (Bates et al., 2015). LMMs for both behavioural measures were fitted via restricted maximum likelihood parameter estimation. All models included a between-subjects fixed factor of *age group* (YA, OA) and within-subjects fixed factors of *switch status* (stay, switch) and *test perspective* (first person, third person). As the interactions between these factors were of interest, an effects coding scheme was used (Singmann & Kellen, 2019). Therefore, the coefficient for each fixed factor represents the deviation of each factor level from the grand mean as denoted by the intercept. To account for non-independence of observations within subjects, all models included a by-subject random intercept, which is the maximal random effects structure supported for aggregate data (Barr, 2013; Barr et al., 2013). The full model specification, provided in lme4 syntax, is as follows:

```
responseVar ~ ageGroup * switchStatus * testPerspective + (1 | subject)
```

Given the skewed nature of RT data, additional Gamma and inverse Gaussian generalised LMMs were run on median RT (Lo & Andrews, 2015). These models assumed linear relationships between response and predictor variables (i.e., specified identity link functions) and shared the same fixed factors as the standard LMMs. However, as they initially failed to converge using the default optimiser, all three models were optimised using bound quadratic approximation. Additionally, these models were (re)-fitted using maximum likelihood parameter estimation to enable valid comparison of different model families. Inferences were drawn from the best-fitting model as determined by the smallest attained Akaike information criterion (AIC) and Bayesian information criterion (BIC) indices.

Model assumptions were checked by examining standard diagnostic residual plots. Outliers were detected using the interquartile range method (i.e., values greater than 1.5x the interquartile range), which makes no distributional assumptions. Analyses were re-run without outlier subjects to assess the robustness of results. *p*-values for LMM fixed effects were computed using Satterthwaite approximations for degrees of freedom (Satterthwaite, 1941), implemented in the ‘lmerTest’ package (Kuznetsova, Brockhoff, & Christensen,

2017). Simulations indicate the Satterthwaite method maintains the Type-I error rate at the nominal alpha level even for smaller sample sizes (Luke, 2017). In comparison, p -values for GLMM fixed effects were obtained from likelihood ratio tests (LRTs). While it should be noted that LRT-derived p -values are moderately anti-conservative (Pinheiro & Bates, 2000), they are preferable to the default t -as- z approach as they are less influenced by sample size (Singmann & Kellen, 2019). Significant interactions were followed up on by performing simple contrasts on the estimated marginal means using the ‘modelbased’ package (Makowski et al., 2020). All tests were two-sided and a canonical alpha level of 0.05 was set. Exact p -values are reported to three decimal places (unless $p < 0.001$).

Image acquisition, pre-processing, and VBM analysis

Scanning took place at the University of Cambridge Medical Research Council Cognition and Brain Sciences Unit using a 3-T Siemens MRI machine with a 32-channel head coil. A whole-brain sMRI image was acquired for each participant using a T1-weighted 3-dimensional magnetisation prepared rapid gradient echo (MP-RAGE) sequence (resolution = 1 x 1 x 1mm isotropic, TR = 2.25s, TE = 3ms, flip angle = 9°, FOV = 256 x 256 x 192mm, GRAPPA acceleration factor = 2). Before pre-processing, sMRI images were visually inspected for artefacts using Mango (v4.1, <https://rui.uthscsa.edu/mango/>). No participants were excluded on this basis.

sMRI images were submitted to a standard VBM pre-processing pipeline (see Figure 5) using the ‘Statistical Parametric Mapping 12’ toolbox (SPM12; <https://www.fil.ion.ucl.ac.uk/spm/>), implemented in MATLAB 2021b (The MathWorks). First, the origin of each image was manually set to the anterior commissure (AC). Images were re-oriented where necessary to align with the common anatomical space of the Montreal Neurological Institute (MNI). Next, images were segmented into grey matter (GM), white matter (WM), and cerebrospinal fluid (CSF) tissue types. To improve inter-subject image alignment, these tissue segmentations were then used to create study-specific group structural templates using diffeomorphic anatomical registration through exponentiated lie algebra (DARTEL; Ashburner, 2007). DARTEL registration was selected based on its superior performance relative to other non-linear deformation algorithms when applied to MRI image registration (Klein et al., 2009). Following registration, images were normalised to common MNI152 space (<http://nist.mni.mcgill.ca/atlas/>). As per recommendations for DARTEL-based VBM (Shen & Sterr, 2012), images were spatially smoothed with an isotropic 8mm full-width at half-maximum (FWHM) Gaussian kernel and modulated to preserve the original

volumes. The default voxel size of 1.5 x 1.5 x 1.5mm was used for processed images. The total intracranial volume (TIV) was computed for each subject by summing the total native space GM, WM, and CSF estimates.

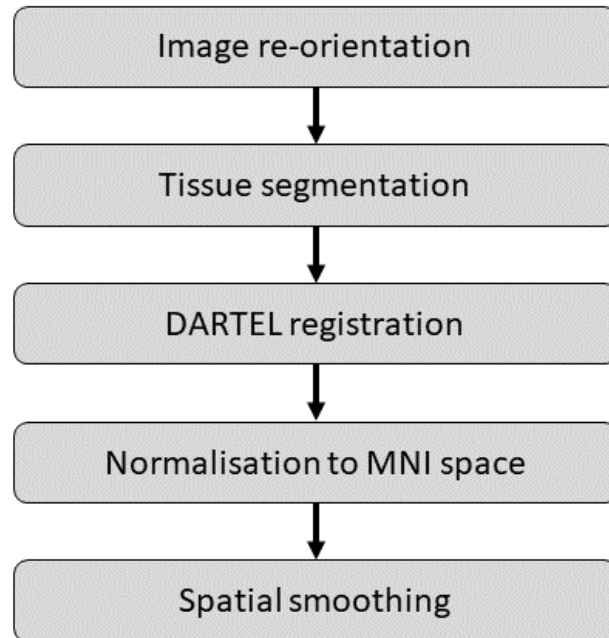


Figure 5. VBM image pre-processing pipeline.

10mm spherical volumes of interest (VOIs) centred on the left AnG (MNI = [-43, -66, 38]) and left precuneus (MNI= [-14, -66, 56]) were chosen before analysis. The *a priori* AnG coordinate was derived from a review of fMRI studies on the parietal lobe and memory (Vilberg & Rugg, 2008), and cTBS thereof has been shown to reduce the reported frequency of first-person ABM recall (Bonnici et al., 2018). The *a priori* precuneus coordinate was obtained from Hebscher et al. (2019), who conducted an *ad hoc* meta-analysis of egocentric cognition to determine a suitable cTBS target site to disrupt ABM recall perspective. These VOIs were limited to the left hemisphere based on meta reviews which indicated primarily left-lateralised recollection-related parietal activity (Vilberg & Rugg, 2008; Rugg & Vilberg, 2013). However, to test the regional specificity and laterality of any potential effects of parietal GMV on memory performance, further exploratory VOI analyses were conducted bilaterally within the full anatomical AnG, precuneus, and hippocampus, which were defined using the Automated Anatomical Labelling Atlas (Tzourio-Mazoyer et al., 2002). The

hippocampus was selected as a control region for this set of VOI analyses as it has previously been associated with allocentric spatial processing in episodic ABM (Hebscher et al., 2018), which should have greater involvement in third person than first person conditions. Finally, exploratory whole brain analyses were conducted to check for relationships of interest in brain regions not identified in any of the more restricted VOI analyses.

To test hypothesised relationships between parietal VOIs and the visual perspective of memory, separate multiple regressions were run on mean MS under each task condition: stay first person, switch first person, stay third person, and switch third person. Participant age, sex, formal education level (in years), and scan-test interval (in years) were entered into the design matrix as covariates of no interest. TIV was also included as a nuisance covariate to account for individual differences in overall head size (Peelle et al., 2012). Both *a priori* and exploratory VOIs were delineated using the Wake Forest University ‘PickAtlas’ SPM12 toolbox (v3.0.2; Maldjian et al., 2003; Maldjian, Laurienti, & Burdette, 2004) and combined into unified masks for small volume correction to simultaneously adjust *p*-values of all voxels within regions of interest for multiple comparisons. Statistical significance was evaluated at the peak level using a familywise error (FWE) corrected threshold of $p < 0.05$, based on Gaussian random field theory (Worsley et al., 1996).

Results

Behavioural results

Demographics. To account for unequal variances between age groups due to unequal sample sizes, two-sided Welch’s two-sample *t*-test were conducted on formal education and scan-test interval (both in years). No significant age difference in education was revealed ($t(36) = 0.96, p = 0.346$). However, the scan-test interval was significantly shorter for YAs than OAs ($t(20.73) = -3.11, p = 0.005$). A two-sided Fisher’s exact test of independence was conducted on the sex count data and found the proportions of men and women did not significantly differ between age groups ($p = 1.0$, *Fisher’s exact test*). See Table 1 for a summary of demographic and cognitive test data for both age groups.

Table 1. Mean (SD in brackets) participant demographic and cognitive test data.

Variable	YAs (<i>n</i> = 17)	OAs (<i>n</i> = 27)	<i>p</i> -value
Age	24.12 (4.27)	74.37 (4.72)	-
Sex	9 male, 8 female	15 male, 12 female	1.0 ^a
Education (years)	18.06 (1.95)	17 (5.20)	0.346 ^b
Scan-test interval (years)	3.09 (0.59) ^c	3.92 (1.03)	0.005 ^b
MoCA score	-	27.70 (1.35)	-
Trails score (parts B – A)	-	33.07 (17.22)	-
Recognition score	-	1.08 (0.32)	-

Note. MoCA, trails, and recognition scores were obtained during scanning.

^a Tested using a two-sided Fisher's exact test of independence.

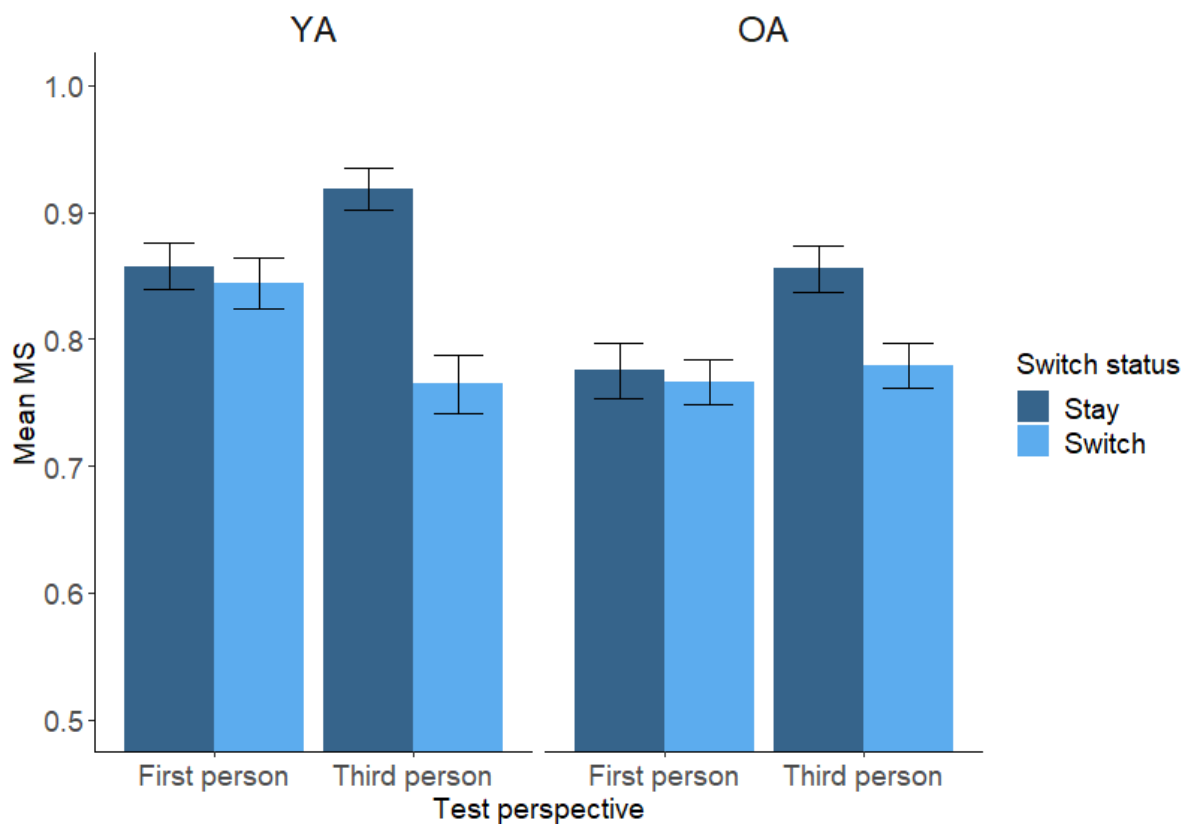
^b Tested using a two-sided Welch's two-sample t-test.

^c *n* = 8 YAs were scanned.

Memory score. To assess the effects of age on object location memory performance in different visual perspectives (see Table 2 for descriptive statistics), a LMM was run on mean MS. This model had a significant intercept ($\beta = 0.82$, $SE = 0.01$, $t(42) = 73.03$, $p < 0.001$) and significant main effects of *age group* ($\beta = 0.03$, $SE = 0.01$, $t(42) = 2.32$, $p = 0.025$) and *switch status* ($\beta = 0.03$, $SE = 0.01$, $t(126) = 6.25$, $p < 0.001$), whereas the main effect of *test perspective* was not significant ($\beta = -0.01$, $SE = 0.01$, $t(126) = -1.86$, $p = 0.066$). Additionally, significant two-way interactions were revealed between *age group* x *test perspective* ($\beta = 0.01$, $SE = 0.01$, $t(126) = 2.79$, $p = 0.006$), *age group* x *switch status* ($\beta = 0.01$, $SE = 0.01$, $t(126) = 2.01$, $p = 0.047$), and *switch status* x *test perspective* ($\beta = -0.03$, $SE = 0.01$, $t(126) = -5.14$, $p < 0.001$). The *age group* x *switch status* x *test perspective* interaction was not significant ($\beta = -0.01$, $SE = 0.01$, $t(126) = -1.81$, $p = 0.072$). The overall pattern of results did not change when outlier subjects (*n* = 7) were removed from this model, except for the three-way interaction, which became non-significant ($\beta = -0.01$, $SE = 0.01$, $t(105) = -1.19$, $p = 0.236$). However, all MS observations identified as outliers seemed reasonable given the task (range = 0.58 – 0.94) and could not be attributed to error. Therefore, all subjects were retained for further analysis. See Figure 6 for barplot of mean MS for each age group and task condition.

Table 2. Mean MS and median RT (SD in brackets) for the object location memory task.

Condition	YAs		OAs	
	MS	RT	MS	RT
First person				
Stay	0.86 (0.08)	6.18 (1.29)	0.78 (0.11)	11.41 (4.20)
Switch	0.84 (0.08)	7.17 (1.75)	0.77 (0.09)	12.51 (5.16)
Third person				
Stay	0.92 (0.07)	6.55 (2.45)	0.86 (0.09)	10.84 (3.98)
Switch	0.76 (0.10)	6.82 (2.43)	0.78 (0.09)	11.63 (3.94)

**Figure 6.** Mean memory score for both age groups across switch status test perspective conditions. Error bars denote standard error of the mean.

To decompose the marginally significant three-way interaction of interest, the simple effects of *age group*, conditioned on *switch status* and *test perspective*, were first examined. YAs had significantly higher MS than OAs in both stay first person trials ($\beta = 0.08$, $SE = 0.03$, $t(96.7) = 2.89$, $p = 0.005$) and switch first person trials ($\beta = 0.06$, $SE = 0.03$, $t(96.7) = 2.20$, $p = 0.030$), supporting an age-related deficit in first-person recall irrespective of the original encoding perspective. While YA performance was also significantly better in stay

third person trials ($\beta = 0.08$, $SE = 0.03$, $t(96.7) = 2.75$, $p = 0.007$), no significant age difference was found in MS in switch third person trials ($\beta = -0.01$, $SE = 0.03$, $t(96.7) = -0.52$, $p = 0.607$), suggesting that third-person recall remains intact in the elderly, but only when memories are originally encoded in a first-person perspective.

Next, the simple effects of *test perspective*, conditioned on *age group* and *switch status*, were probed. Stay first person MS was significantly lower than stay third person MS in both YAs ($\beta = -0.06$, $SE = 0.02$, $t(126) = -2.72$, $p = 0.007$) and OAs ($\beta = -0.08$, $SE = 0.02$, $t(126) = -4.53$, $p < 0.001$), indicating that first-person recall is generally less accurate than third-person recall when the test perspective is congruent with the encoding perspective. In contrast, switch first-person MS was significantly higher than switch third person MS in YAs ($\beta = 0.08$, $SE = 0.02$, $t(126) = 3.56$, $p < 0.001$) but not in OAs ($\beta = -0.01$, $SE = 0.02$, $t(126) = -0.75$, $p = 0.456$). This result suggests that only YAs had greater relative difficulty in recalling object locations from a third-person perspective when encoded from a first-person perspective.

The simple effects of *switch status*, conditioned on *age group* and *test perspective*, were then finally investigated. MS did not significantly differ between switch and stay trials when the test perspective was first person in both YAs ($\beta = 0.01$, $SE = 0.02$, $t(126) = 0.59$, $p = 0.566$) and OAs ($\beta < 0.01$, $SE = 0.02$, $t(126) = 0.52$, $p = 0.603$). By comparison, MS in stay third person trials was significantly higher than MS in switch third person trials in both YAs ($\beta = 0.15$, $SE = 0.02$, $t(126) = 6.87$, $p < 0.001$) and OAs ($\beta = 0.08$, $SE = 0.02$, $t(126) = 4.30$, $p < 0.001$). Taken together, these results indicate the existence of a directional switch cost for third-person recall irrespective of age, which was greater in magnitude for YAs than OAs, however.

An exploratory LMM was run on MS in the OAs to control for general age effects on executive and memory abilities. Accordingly, the nuisance variables *trials score* and *recognition score* were included as additive (non-interacting) fixed covariates to account for their total contribution to variability in MS ($\sim$ `switchStatus * testPerspective + recognitionScore + trialsScore + (1 | subject)`). This model had a significant intercept ($\beta = 0.69$, $SE = 0.61$, $t(23) = 11.33$, $p < 0.001$) and revealed *recognition score* to be a significant predictor of MS in the elderly ($\beta = 0.94$, $SE = 0.04$, $t(23) = 2.15$, $p = 0.043$) but not *trials score* ($\beta < 0.01$, $SE < 0.01$, $t(22) = 0.33$, $p = 0.741$). Critically, the *switch status* x *test perspective* interaction remained significant ($\beta = -0.02$, $SE = 0.01$, $t(75) = -2.28$, $p =$

0.025) as did the main effects of *switch status* ($\beta = 0.02$, $SE = 0.01$, $t(75) = 3.35$, $p = 0.001$) and *test perspective* ($\beta = -0.02$, $SE = 0.01$, $t(75) = -3.55$, $p < 0.001$). These results indicate the performance of OAs in the object location memory task cannot fully be explained by general age-related executive dysfunction or memory impairment.

Response time. The effects of age on response latencies (see Table 2 for descriptive statistics) were then examined by running a standard LMM, as well as additional Gamma and inverse Gaussian models with identity link functions, on median RT. Inspection of diagnostic residual plots for the standard LMM revealed a leptokurtic distribution and noteworthy heteroscedasticity when plotted against fitted values. The poor appropriateness of the LMM for modelling RT was also supported by AIC and BIC model fit indices, both of which favoured the Gamma model (see Table 3). Therefore, this model was selected for interpretation.

Table 3. AIC and BIC model fit indices comparing different RT models

Model	AIC	BIC
LMM	816.28	854.05
Gamma	762.79	794.26
Inverse Gaussian	774.71	806.19

Note. Both Gamma and Inverse Gaussian LMMs used an identity link function.

In the Gamma model, the intercept was significant ($\beta = 9.68$, $SE = 0.69$, $t = 14.08$, $p < 0.001$). There were significant main effects of *age group* ($\beta = -2.31$, $SE = 0.68$, $t = -3.42$, $p < 0.001$) and *switch status* ($\beta = -0.35$, $SE = 0.12$, $t = -2.96$, $p = 0.003$) whereas the main effect of *test perspective* was not significant ($\beta = 0.24$, $SE = 0.12$, $t = 1.93$, $p = 0.054$). No significant two-way interactions were found between *age group* x *test perspective* ($\beta = 0.08$, $SE = 0.12$, $t = 0.64$, $p = 0.523$), *age group* x *switch status* ($\beta = 0.07$, $SE = 0.12$, $t = 0.61$, $p = 0.542$), or *test perspective* x *switch status* ($\beta = -0.06$, $SE = 0.12$, $t = -0.49$, $p = 0.624$). The *age group* x *switch status* x *test perspective* interaction was similarly non-significant ($\beta = -0.03$, $SE = 0.12$, $t = -0.24$, $p = 0.811$). Excluding outlier subjects ($n = 5$), four of whom were OAs that exceeded the YA 15s response deadline, had no effect on the pattern of results. See Table 2 for descriptive statistics and Figure 7 for barplot of mean RT by age group and task condition.

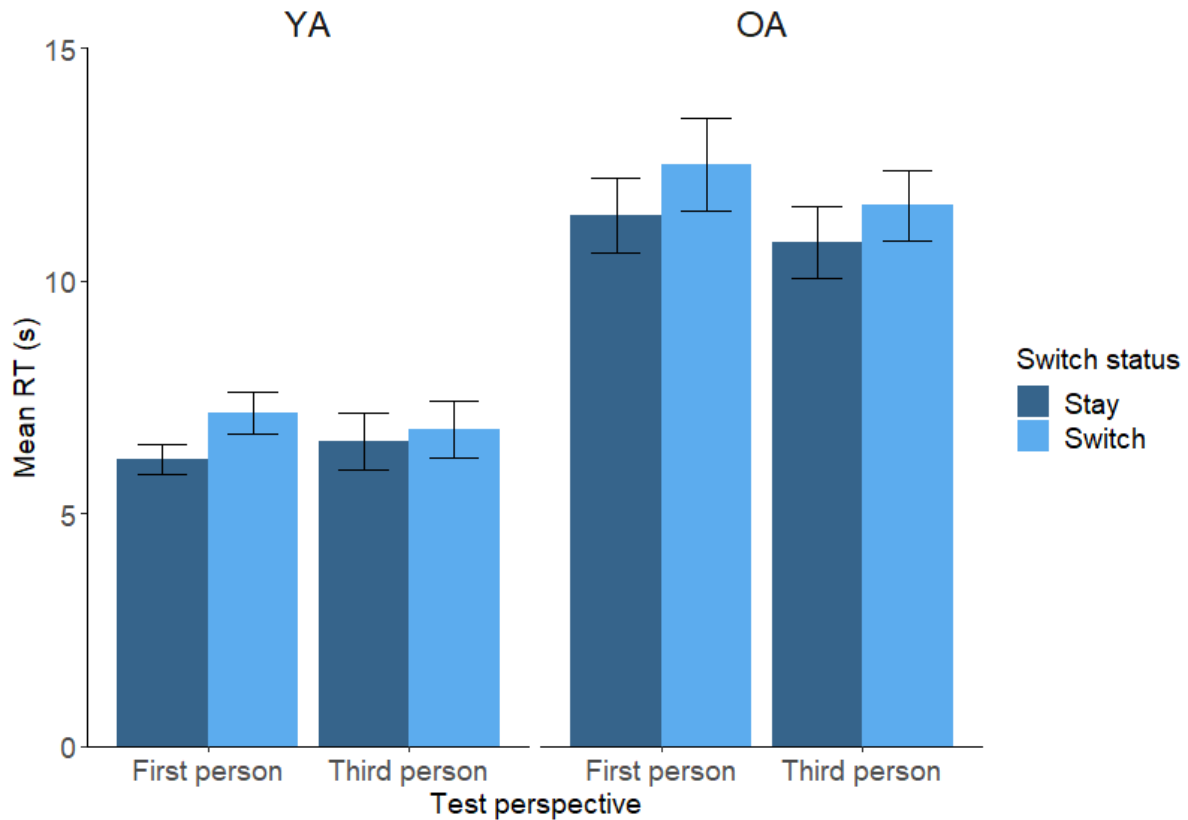


Figure 7. Means of median RTs for both age groups across switch status and test conditions. Error bars denote standard error of the mean.

VBM results

Two-sample *t*-tests assuming unequal variance were first conducted to identify potential age-related group differences in *a priori* parietal VOIs, controlling for nuisance effects of sex, education, scan-test interval, and TIV. As predicted, OAs were revealed to have significantly less GM volume than YAs in both the left AnG ($t(29) = 8.15, p < 0.001$, peak MNI = [-51, -63, 42]) and the left precuneus ($t(29) = 7.04, p < 0.001$, peak MNI = [-20, -69, 56]). Multiple regressions were then performed in the OAs to test hypothesised relationships between parietal GM volume and memory performance under the different perspective conditions, after controlling for nuisance effects of age, sex, education, scan-test interval, and TIV. Consistent with subserving the specific adoption of a first-person recall perspective, significant positive associations with switch first person MS were found in OAs for left AnG ($t(20) = 5.64, p = 0.002$, peak MNI = [-34, -66, 44]) and left precuneus ($t(20) = 4.18, p = 0.032$, peak MNI = [-10, -75, 54]) VOIs. Only the left AnG result (for visualisation, see Figure 8) survived a Bonferroni-corrected threshold accounting for separate analysis of the four task conditions ($\alpha = 0.0125$). No further significant associations were found

between either *a priori* VOI and the other task conditions (all $t_s < 2.84$ and $p_s > 0.288$). In the exploratory VOI analyses, no significant positive associations were found between memory performance and bilateral AnG, precuneus, or hippocampus GMV (all $t_s < 4.35$ and $p_s > 0.274$), including switch first person MS and left AnG GMV ($t(20) = 5.24$, $p = 0.056$, peak = $[-35, -68, 44]$). Finally, no significant positive associations were found in the whole brain analyses (all $t_s < 5.06$ and $p_s > 0.171$).

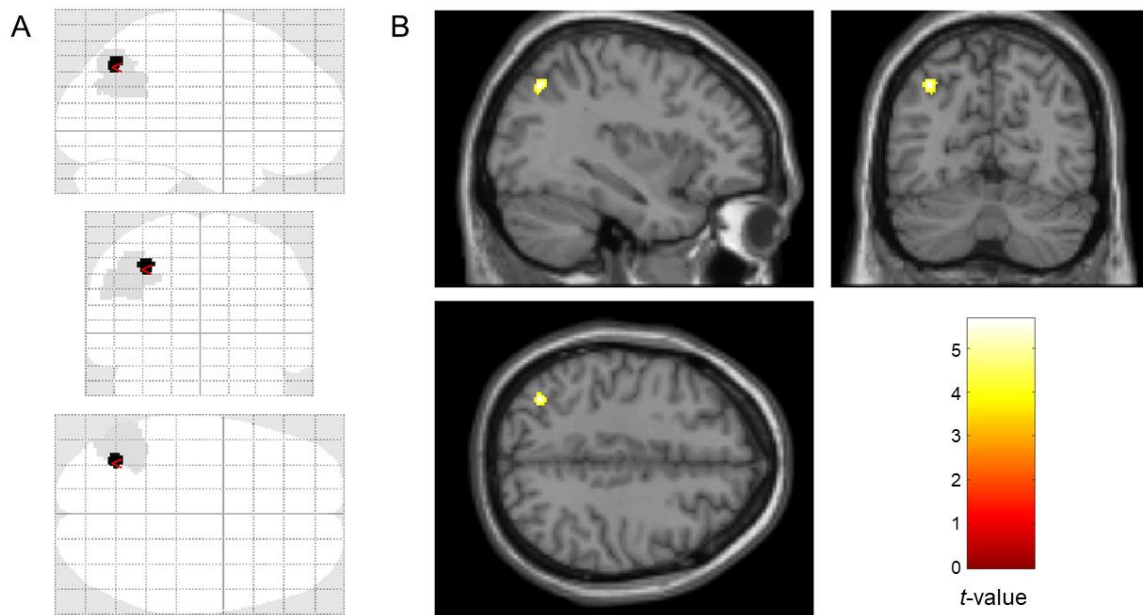


Figure 8. Left AnG grey matter volume showing a significant positive correlation with switch first person trial performance in the *a priori* VBM analysis. A) Glass brain showing the AnG cluster (black) overlaid on the whole anatomical region as defined by the Automated Anatomical Labelling Atlas (grey). B) t -map of voxels within the AnG cluster on the SPM12 T1 single subject template. Note that both subfigures were created using the ‘xjview’ MATLAB toolbox (v10.0; <https://www.alivelearn.net/xjview>), centred on the significant FWE-corrected peak AnG coordinate (MNI = $[-34, -66, 44]$), and visualised at an uncorrected threshold of $p < 0.001$.

Discussion

This chapter investigated the effects of age on first-person episodic recall and its neuroanatomical correlates in the elderly using a custom object location memory task and VBM. An age-related deficit in first-person recall performance was evident regardless of the original encoding perspective. Within both age groups, first-person recall was less accurate than third-person recall when encoded in the same perspective. However, only the YAs showed a difference in accuracy between switch first person and switch third person trials. A switch cost was apparent in RT for both age groups as predicted, but accuracy was reduced

only when perspective was switched from a first-person to a third-person perspective and not vice versa. Moreover, this switch cost was unexpectedly greater in the YAs than the OAs. Importantly, the overall pattern of behavioural results did not change in the OAs after controlling for general executive and memory abilities. Regarding the VBM results, the OAs had less parietal GMV overall than the YAs. In the OAs, GMV in both the left AnG and precuneus was positively associated with switching from a third person encoding perspective to a first person retrieval perspective, although this result was more robust in the AnG.

Consistent with predictions, the OAs were less able to accurately recall object locations from a first-person perspective than a third-person perspective. This harmonises with the results of Ladyka-Wojcik et al. (2021), who tested OAs (but not YAs) in a similar 3D spatial memory task. In the present study, YAs were included for comparison and showed a similar pattern of performance to the OAs, but with first-person recall being more impaired in the OAs than the YAs, original encoding perspective notwithstanding. Moreover, the age difference found here can be more confidently attributed to differences in recall perspective rather than viewpoint-specific differences in object identifiability. This was achieved for both targets and distal landmarks by presenting the same object face regardless of the perspective. However, further work is needed to replicate this finding and explore the complex relationship between recall perspective and recollective experience, which might break down with age (Folville et al., 2021). For example, Kapsetaki et al. (2022) recently found a correlation in YAs but not OAs between the ability to identify one's first-person encoding perspective in a 3D scene memory task and the reported episodic richness of ABM. This relationship was not present in either age group when they were tested by Kapsetaki et al. using standard 2D photographic stimuli, suggesting more immersive and naturalistic memory tasks should be used in the investigation of subjective memory experience, which was not directly examined in the present study. It should also be acknowledged that the different perspective conditions were not equivalent in terms of daily experience as events are typically encoded and retrieved in first person while a third-person perspective can take multiple forms (e.g., a top-down bird's eye view as in the present study, an over-the-shoulder view, or another individual's first-person viewpoint; McCarroll, 2018). Therefore, future work should account for these factors and how they might influence subjective as well as objective aspects of episodic memory.

As in Ladyka-Wojcik et al. (2021), a directional switch cost was also found in the OAs on accuracy for object locations recalled from a third-person perspective but encoded

from a first-person perspective. This is consistent with previous evidence that OAs may be particularly impaired at perspective switching when environments navigated in first person are tested allocentrically in spatial recall tasks (Harris, Wiener, & Wolbers, 2012). This is also broadly consistent with findings in YAs of higher perceptual switch costs in allocentric versus egocentric spatial reference frames (Lv & Hu, 2020) and reduced memory accuracy when shifting from a first-person own-eyes perspective to a third-person observer one (Marcotti & St. Jacques, 2018; Marcotti & St. Jacques, 2022). Ladyka-Wojcik et al. interpreted this result as evidencing an allocentric learning advantage in the elderly, possibly due to the greater flexibility afforded by allocentric spatial encoding (Blackmore, 1987; Rice & Rubin, 2011). In the present study, however, both age groups showed the same overall patterns of performance for switch trials, yet the directional switch cost to accuracy was unexpectedly greater in the YAs than the OAs. Furthermore, a general switch cost that was not modulated by test perspective was evident when examining RT, indicating a subtler deficit in switch first person trials. When compared against the YAs, the OAs were no less accurate in this condition.

Considering the behavioural results together, the generally worse first-person perspective memory performance observed in the OAs might reflect difficulty in binding spatial information across multiple vantage points (Montefinese et al., 2015). Indeed, normal ageing has been shown to impair the binding of object, spatial, and temporal contextual elements of episodes more generally in so-called What-Where-When memory tasks (Kessels, Hobbel, & Postma, 2009; Mazurek et al., 2015; Varela, Evdokimidis, Potagas, 2021). While viewpoint was technically allowed to vary in both perspective conditions of the present task (i.e., subjects could rotate the camera when in a first-person perspective and zoom it in or out when in a third-person perspective), the spatial relationship between target and landmark objects would nevertheless have remained more stable when viewed from different third-person vantage points. In contrast, the greater difficulty in binding object locations within an egocentric encoding framework might then have been reduced in the OAs when a more reliable allocentric reference frame was provided during third-person recall. This would accord with observations that memory in the elderly can benefit from increased levels of external support (e.g., Park & Shaw, 1992; Perlmutter, 1979; for review see Lindenberger & Mayr, 2014).

The greater relative deficit in first-person recall found in the OAs may also reflect a more general age-related decline in embodied cognition (see Costello & Bloesch, 2017;

Kuehn et al., 2018; Vallet, 2015 for reviews). For example, OAs perform worse than YAs in egocentric mental rotation tasks that typically require visuospatial bodily self-rotation versus those involving object rotation (de Simone et al., 2013; Devlin & Wilson, 2010; Inagaki et al., 2002; Jansen & Kaltner, 2014; Kaltner & Jansen, 2016). Furthermore, OAs seemingly have a reduced capacity for motor imagery (for review, see Saimpont, et al., 2013), particularly when simulating actions from a first-person rather than third-person perspective, which in the former case are also often rated as less vivid (Mulder et al., 2007; Saimpont et al., 2012). Regarding spatial memory, OAs are less accurate than YAs at reconstructing environments when encoded in first person but not in third person (Yamamoto & DeGirolamo, 2012), but may nevertheless prefer an egocentric navigation strategy (Rogers, Sindone, & Moffat, 2012), possibly by virtue of the lower demand it is assumed to place on spatial transformations (Colombo et al., 2017). Thus, future work should endeavour to separate potential age differences in spatial strategy use from potential age differences in recall perspective.

It should be cautioned that many OAs withdrew from the present study ($n = 12$), most of whom did so due to task difficulty or difficulty comprehending task requirements ($n = 7$). Therefore, it is possible that the true OA performance levels were overestimated in this study. Conversely, while no clinically noteworthy cognitive decline was detected in the OAs using the MoCA during the scanning period, and none reported diagnoses of relevant conditions at the time of testing, it is also possible that any age differences observed in the current study might be contaminated by some degree of undetected neurological pathology. Finally, it should be acknowledged that age differences in location memory accuracy might also be confounded by age differences in the ability to accurately report location memory. However, all OAs reported normal or corrected-to-normal vision and were allowed to respond at their own pace, which together should have mitigated the influence of motor or perceptual age differences on memory accuracy. Supporting this, the OAs took approximately twice as long as YAs to respond yet did so with above-chance accuracy in all conditions. Additionally, the OAs were just as able as the YAs to recall object locations in switch third person trials, despite worse performance relative to stay third person trials in both age groups. Furthermore, age-related spatial memory deficits have previously been found in both egocentric and allocentric spatial reference frames using real-world tasks as well as virtual ones (Fernandez-Baizan et al., 2019; Fernandez-Baizan, Arias, & Mendez, 2020). However,

future studies should ideally still take place in the laboratory, where control tasks can be administered more easily.

Turning to the VBM results, accuracy in switch first person trials was positively associated in the OAs with GMV in left AnG and precuneus VOIs, indicating a role for both regions in the adoption of a first-person perspective during recall rather than first-person recall more generally. This relationship was most robust in the left AnG, which remained significant after correcting for multiple tests, but failed to remain significant when the search volume was expanded in the exploratory VOI and whole brain analyses. Contrary to expectations based on previously observed associations between hippocampal volume and allocentric processing in episodic ABM (Hebscher et al., 2018), no association was found between third-person memory performance and GMV of medial temporal structures such as the hippocampus, which served as an explicit control region in the exploratory VOI analyses. However, task difficulty was not fully matched across the different perspective conditions, with both age groups performing near ceiling in stay third person trials. Accordingly, this null result might simply reflect insufficient variability to detect an effect of GMV on memory performance in this condition. Thus, it should be cautioned that the anatomical specificity of the present findings is uncertain.

While the VBM results are tentative, they are broadly consistent with recent observations of concomitant activation within the left AnG and precuneus during perspective shifting (Iriye & St. Jacques, 2018; Marcotti & St. Jacques, 2018; St. Jacques, Szpunar, & Schacter, 2017). How then might the two parietal regions differ functionally? In line with its well-established role in mental imagery, the precuneus might first instantiate vivid first-person visual images during retrieval (Richter et al., 2016). These representations might then reach consciousness through AnG-mediated multisensory integration within a broader egocentric context (Bonnici et al., 2018) and online maintenance in working memory (Humphreys et al., 2021). Under this view, the lack of association between stay first person trial accuracy and precuneus volume in the present study may be explained by insufficient evocativeness of the first-person episodes produced by the current task. Although its 3D and immersive nature better captured some of the properties of veridical episodes when compared against more standard 2D tasks, the content of episodes generated from this task were lacking in richness and variety. Therefore, more naturalistic 3D tasks might bring greater clarity to this issue.

Although the OA sample size in this study is within the typical range for VBM analyses, it is probable that the large scan-test interval in this group reduced sensitivity. The large number of covariates relative to subjects likely also decreased statistical power, and not all may be necessary. For example, TIV may account for both sex-related and individual variability in head size (Raz et al., 2004). Nevertheless, a significant association was found between GMV in the parietal VOIs and switch first person trial performance after controlling for these covariates, all of which are standard for the type of analysis reported here. Given the apparent importance of both the left AnG and precuneus in first-person recall, the lack of a relationship in the current study between GMV in either parietal VOI and stay first person trial performance is intriguing. While null results are difficult to interpret, it is possible that the general decline in parietal GMV observed in the OAs relative to the YAs diminished this relationship, which might be stronger earlier in life. Indeed, analysis of both FreeSurfer (Hebscher, Levine, & Gilboa, 2018) and VBM (Freton et al., 2013) precuneus volumes has revealed positive associations with first-person ABM recall in healthy YAs. To the best of my knowledge, no study until the present one has been conducted on AnG GMV. However, similar relationships should be detectable in principle, especially in neurologically healthy YAs.

Finally, the lack of a significant association between first-person recall and right-hemisphere parietal GMV is interesting given the possibly greater right lateralisation of egocentric cognition (Iachini et al., 2009; Rorden et al., 2012; Russell et al., 2019; Schindler & Bartels, 2013; Weniger et al., 2009). Russell et al. (2019) recently showed right-damaged parietal patients to be less able than age-matched controls at identifying their own egocentric encoding perspective during recall of 3D scenes. In contrast, Ciaramelli et al. (2010b) found left parietal lesion patients to be more impaired on egocentric spatial navigation tasks than patients with right parietal damage. However, both patient groups in Ciaramelli et al.'s study also reported reduced first-person re-experiencing during recall of learned routes, suggesting both hemispheres, and possibly the interaction between them, may be important to subjective memory reliving. Supporting this possibility, Russell et al. (2019) used multi-voxel pattern analysis to show fMRI activity patterns in bilateral parietal regions including the AnG are sensitive to the same perspective shift judgements made by neurologically healthy OAs as those performed by their parietal patients, although a smaller set of left parietal regions were involved in such judgements in YAs. This latter finding is consistent with frequent observations in the wider neuroimaging literature of more left-lateralised parietal

involvement during recollection (for reviews, see Vilberg & Rugg, 2008; Rugg & King, 2017; Rugg & Vilberg, 2013) and possibly its subjective experience (e.g., Bonnici et al., 2016; 2018; Yazar, Bergström, & Simons, 2014; 2017). Furthermore, disrupted left AnG function resulting from non-invasive brain stimulation has also been shown to reduce first-person (egocentric) ABM (Bonnici et al., 2018). In the future, non-invasive brain stimulation techniques should be used to isolate the causal contributions of parietal regions such as the AnG and precuneus, as well as both hemispheres, to subjective episodic memory experience (as intended before the pandemic).

In conclusion, the experiment presented in this chapter tested whether first-person (egocentric) episodic recall is impaired in normal ageing using a custom 3D object location memory task that manipulated both encoding and retrieval perspective in healthy YAs and OAs. A general age-related deficit in first-person recall was found. Third-person recall was impaired to lesser degree and only when the encoding perspective was also third person. Furthermore, the ability of OAs to adopt a first-person perspective during recall was positively associated with the GMV of both the left AnG and the precuneus. No neuroanatomical correlate was identified for first-person recall more generally. Finally, the GMV of both parietal regions was found decline with age. Future work should examine the relationship between recall perspective and subjective memory experience, as well as how that relationship might change during normal ageing.

Chapter 4: The Visuospatial Perspective of Episodic Memory in Aphantasia

The study presented in the final experimental chapter of this thesis investigated whether aphantasics, individuals with self-reported voluntary mental imagery deficits, are impaired at episodic memory recall from a first-person versus third-person visuospatial perspective. The 3D object location memory task used in the study reported in the previous chapter was modified for the present one to allow objective and subjective measures of memory for both object and spatial features to be taken under different perspective conditions. Aphantasic participants were unimpaired relative to controls on all measures of objective memory performance, but exhibited weaker experience of imagery and lower overall subjective vividness ratings on the memory task. These results add to recently emerging evidence for a possible subtype of aphantasia characterised by differences in the conscious awareness of mental imagery, rather than a deficit in mental imagery itself. In both groups, however, object features were remembered in higher fidelity when studied and tested in first person versus third person, suggesting a first-person perspective might facilitate subjective memory reliving by enhancing the representational quality of scene contents.

Introduction

In most individuals, mental imagery—the ability to represent sensory information in the absence of perception (Pearson et al., 2015)—pervades subjective mental experience. For example, mental imagery allows us to direct our senses inward and ‘see’ with our mind’s eye the contents of a dream or ‘hear’ with our mind’s ear the voice of a loved one. More concretely, visual mental imagery is thought to support numerous cognitive faculties, particularly visual working memory and episodic processing (Pearson, 2019), where visual mental imagery is typically evoked during the recollection of personal events (i.e., episodic memory) or while imagining future or counterfactual ones (i.e., episodic simulation) (Schacter et al., 2012; Schacter & Madore, 2016). Furthermore, the subjective richness of episodic processing has been associated with visual mental imagery (D’Argembeau & van der Linden, 2006), the capacity for which can be trained to possibly improve autobiographical memory (ABM) in a variety of conditions (Ernst et al., 2013; Hussey et al., 2013; Vranic, Martincevic, & Borella, 2021). Although mental imagery has long been reported to vary across individuals (Galton, 1888), the study of mental imagery extremes has only recently received renewed scientific interest. Of relevance to this study, a minority of individuals self-report a profound weakness in, or a complete inability to form, voluntary visual mental imagery. This phenomenon has recently been termed ‘aphantasia’ (Zeman, Dewar, & Della Sala, 2015).

Aphantasia is estimated to occur in approximately 2-4% of the general population and is usually congenital (Dance, Ipser, & Simner, 2022; Faw, 2009; Zeman, Dewar, & Della Sala, 2015; Zeman et al., 2020), although it can also be acquired through psychiatric disturbances or brain injury (Bartolomeo, 2008; Farah, 1984; Zago et al., 2011; Zeman et al., 2010). Moreover, while aphantasia is typically identified via subjective self-reports such as with the Vividness of Visual Imagery Questionnaire (VVIQ; Marks, 1973), the condition is considered by many to reflect a true deficit in voluntary mental imagery ability rather than impaired metacognition. For instance, aphantasics show little imagery-based priming in binocular rivalry tasks (Keogh & Pearson, 2018), where the separate presentation of different images to each eye normally results in the dominance of one and suppression of the other from consciousness (Pearson, 2014). Imagining previously viewed images after a delay period also fails to elicit a pupillary light reflex in aphantasics, which is an automatic physiological response that indexes perceptual luminance but has also been demonstrated to track the trial-by-trial strength and vividness of mental imagery in those with typical mental

imagery (Kay et al., 2022). Similarly, aphantasics show flat-line levels of skin conductance while imagining fear-inducing scenarios, unlike controls (Wicken, Keogh, & Pearson, 2021). However, recent evidence suggests that not all aspects of visual mental imagery are impaired equally in people with aphantasia.

Visual mental imagery is thought to be dissociable into object and spatial subcomponents (Farah et al., 1988; Levine, Warach, & Farah, 1985), evoking the behavioural and neural distinctions between the ventral (i.e., “what pathway”) and dorsal (i.e., “where pathway”) processing streams (Hickok & Poeppel, 2004). Indeed, the primary visual cortex is frequently associated with both visual perception and visual mental imagery, highlighting the overlap between these two faculties (Bartolomeo, 2000; Ganis, Thompson, & Kosslyn, 2004; Kosslyn, Ganis, & Thompson, 2001; Pearson, 2019; Pearson et al., 2015; Winlove et al., 2018). Object imagery refers to low-level perceptual visual representations of attributes such as size, shape, colour, or brightness. By contrast, spatial imagery relates to the representation of environments including the spatial configurations among or within objects, their locations, and movements. On self-report measures such as the Object-Spatial Imagery Questionnaire (Blajenkova, Kozhevnikov, & Motes, 2006), aphantasics indicate difficulties with object, but not spatial, imagery (Bainbridge et al., 2021; Dawes et al., 2020; 2022; Keogh & Pearson, 2018). Furthermore, both acquired (Zeman et al., 2010) and congenital (Pounder et al., 2022) aphantasics are as accurate as controls on mental rotation tasks, which require manipulation of visuospatial representations. Based on such evidence, some have suggested aphantasia to dissociate along the classic “what” and “where” processing pathways (Pearson, 2019). However, on mental rotation tasks, aphantasics generally do not exhibit the expected linear increase in response with increased angular disparity between different presented object orientations (Pounder et al., 2022; Zeman et al., 2010; but see Zhao et al., 2022), suggesting alternative strategy use in tasks tapping spatial imagery also. Similarly, the rotation-related negativity, an electrophysiological correlate of spatial transformations, has been shown to be absent in a patient with acquired aphantasia (Zhao et al., 2022). Related to this, aphantasics also often score higher on autism traits including difficulties with theory of mind (Dance et al., 2021), which is thought to depend on the ability to adopt alternative visuospatial perspectives (Conson et al., 2015; Gauthier et al., 2018; Kessler & Wang, 2012; Pearson et al., 2014).

While aphantasia is defined by deficits in visual (i.e., object) imagery, other areas of cognition also seem to be impaired. For example, many aphantasics report difficulty with

recognising faces (Dawes et al., 2020), possibly due to their visual mental imagery deficits (Grüter et al., 2009). Most strikingly, however, most aphantasics report remarkable deficits in episodic memory and simulation, as suggested by the importance of mental imagery in these domains. In the first large-scale questionnaire-based study to explore the cognitive profile of aphantasia, aphantasics reported less vivid and phenomenologically rich autobiographical memories (ABMs) and imagined future scenarios than controls (Dawes et al. (2020)). In a recent large sample online study, Bainbridge et al. (2021) used a 2D drawing task to show that aphantasics are impaired at recalling object, but not spatial, memory features, consistent with the overall pattern of their reported imagery deficits. However, mental imagery often involves the adoption of particular visuospatial perspectives (Libby & Eibach, 2011), which has not yet been investigated in aphantasia. Indeed, a first-person self-referential (i.e., egocentric) visuospatial perspective is thought to play an important role in subjective memory reliving and broader autonoetic consciousness (Simons, Ritchey, & Fernyhough, 2022; Zaman & Russell, 2022). Furthermore, while the primary visual cortex has been posited as a likely substrate for the visual buffer (Kosslyn, 2005), and transcranial magnetic stimulation thereof has been shown to disrupt visual mental imagery (Kosslyn et al., 1999), patients with damage to the primary visual cortex do not always show imagery deficits (Bridge et al., 2010; 2012) whereas patients whose primary visual cortex is undamaged can (Moro et al., 2008), calling into question the necessity of the region in visual mental imagery. Considering this apparent inconsistency, some have proposed primary visual cortex to be recruited only for high-resolution visual mental imagery (Daselaar et al., 2010; Kosslyn & Thompson, 2003). However, other regions have been implicated in visual mental imagery including the precuneus, which may be preferentially engaged during episodic recall involving vivid first-person visual mental imagery (Cavanna & Trimble, 2006; Fletcher et al., 1995; Fulford et al., 2018; Gardini et al., 2006).

The study presented in this chapter tested whether first-person (egocentric) episodic recall is impaired in people with aphantasia. A mixed design was employed in which aphantasic and non-aphantasic control participants completed a novel 3D object and spatial memory task that manipulated visuospatial perspective. The spatial memory component of the task was adapted from the object location memory task presented in Chapter 3, which entailed studying object locations in familiar virtual environments from either a first-person or third-person perspective. As in the previous study, the perspective from which these object locations were later tested was additionally varied between the same and alternative study

perspective to test whether aphantasics are impaired at manipulating spatial representations, based on inconclusive findings from mental rotation tasks (Pounder et al., 2022; Zeman et al., 2010; Zhao et al., 2022). This resulted in the following four spatial memory conditions: stay first person (i.e., studied and tested in a first-person perspective), switch first person (i.e., studied in third person but tested in first person), stay third person (i.e., studied and tested in a third-person perspective), and switch third person (i.e., studied in first person but tested in third person). In the current study, however, object memory was additionally assessed by varying the colour hue of studied objects, which participants then had to reproduce during test in a continuous report task (Richter et al., 2016). Thus, there were two object memory conditions: study first person and study third person.

Given the similarity between the spatial memory component of the current task and the object location memory task in Chapter 3, a similar overall pattern of performance was expected. Specifically, first-person spatial recall was predicted to be generally less accurate than third-person spatial recall. Moreover, an asymmetric perspective switch cost was predicted, with switch third person trials being recalled less accurately than switch first person trials, relative to the respective perspective stay trials (Marcotti & St. Jacques, 2018; Marcotti & St. Jacques, 2022). Despite benefitting spatial memory accuracy (Iriye & St. Jacques, 2021), third-person recall was predicted to be rated as less vivid in general than first-person recall (Libby & Eibach, 2002). In aphantasics, the limited previous literature means that predictions must be speculative, but the subjective vividness of recall was predicted to be rated lower overall when compared against controls. Based on the importance of a first-person visuospatial perspective in subjective episodic memory experience (Simons, Ritchey, & Fernyhough, 2022; Zaman & Russell, 2022), which has been reported to be diminished in people with aphantasia (Dawes et al., 2020), first-person (egocentric) spatial memory performance was predicted to be lower in aphantasics relative to controls. In contrast, third-person spatial memory was predicted to be relatively unimpaired in aphantasics (Bainbridge et al., 2021). Finally, aphantasics were predicted to have generally worse object memory performance than controls, in based on previous observations of imagery (Dawes et al., 2020) and memory deficits in this domain (Bainbridge et al., 2021).

Materials and Methods

Participants

Participants were assigned to aphantasic and non-aphantasic control groups based on their score on the VVIQ, which is a widely used non-clinical self-report measure of visual

mental imagery experience (Marks, 1973). The VVIQ assesses how vividly participants are able to visualise different scenarios involving people and scenes and shows high reliability and construct validity across different versions (Campos & Pérez-Fabello, 2009; McKelvie, 1995). As there is currently no consensus on the appropriate cut-off score to identify aphantasia, a VVIQ score ≤ 32 was used for the aphantasic sample in the present study (see Figure 1 for histogram of VVIQ scores in both imagery groups). While more conservative thresholds have been used (e.g., ≤ 25 in Bainbridge et al., 2021), a cut-off score of 32 nonetheless corresponds to very weak visual mental imagery across all questionnaire items and was used recently in an influential questionnaire-based cognitive characterisation of aphantasia (Dawes et al., 2020)

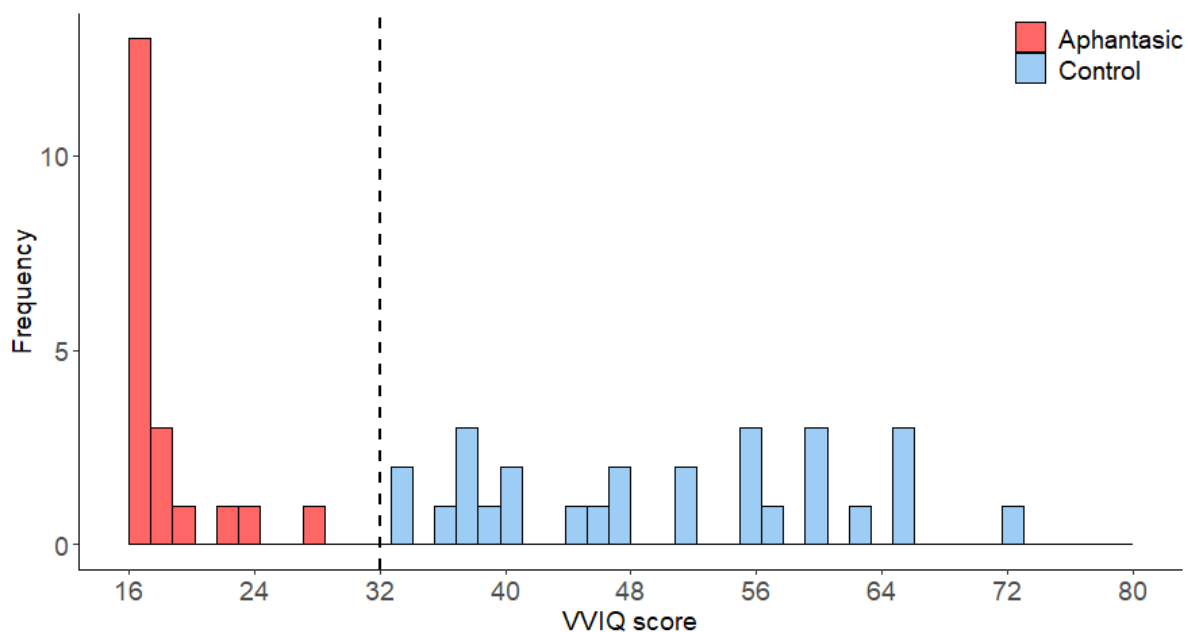


Figure 1. Histogram of VVIQ scores for aphantasic and control groups. The dotted vertical line indicates the *a priori* VVIQ cut-off score of 32 used to define aphantasia in this study.

Aphantasics. 20 congenitally aphantasic individuals (35% male) with a mean VVIQ score of 17.70 (SD = 3.18, range = 16 – 28), mean age of 26.70 (SD = 5.01, range = 18 – 35), and an undergraduate median education level were included in the analyses. The self-reported imagery experience of the current aphantasics closely aligned with that documented in large sample surveys of the condition (mean VVIQ = 17.50; n aphantasics = 2267; Dawes et al., 2020; Zeman et al., 2020). Furthermore, the majority of aphantasic participants ($n = 14$) reported a complete absence of visual mental imagery (VVIQ = 16). An additional eight aphantasic participants were tested but excluded due to study non-completion, excessive anticipatory responses, or below chance mean performance in the object or spatial

components of the memory task, averaged across conditions. Aphantasic participants were recruited from various online aphantasic communities on Reddit and Facebook.

Controls. 27 non-aphantasic individuals (44% male) with a mean VVIQ score of 51.37 (SD = 11.20, range = 34 – 72), mean age of 27.73 (SD = 5.60, range = 20 – 35), and an undergraduate median education level were included in the analyses. No control participants had VVIQ scores indicating the opposite extreme of mental imagery experience to aphantasia, hyperphantasia (VVIQ ≥ 75 ; Zeman, Dewar, Della Sala, 2015; Zeman et al., 2020). A further 17 control participants were tested but excluded from analysis due to early withdrawal from the study, excessive anticipatory responses, or below chance mean performance across conditions in either component of the memory task. All control participants were recruited from the online testing platform Prolific (www.prolific.co).

All participants reported native-like English proficiency, had normal or corrected-to-normal colour vision, and confirmed they had no current or historical diagnoses of developmental, psychiatric, or neurological conditions. Participants gave informed consent prior to testing and were remunerated in a manner approved by the University of Cambridge Human Biology Research Ethics Committee. As with the study presented in Chapter 3, pandemic-related disruptions prevented attainment of the intended group sample sizes ($n = 32$). Nevertheless, the samples collected here are comparable in size to those of many other task-based studies of aphantasia (e.g., Keogh & Pearson, 2018; Keogh, Wicken, & Pearson, 2021; Pounder et al., 2022).

Stimuli

Stimuli consisted of 80 target and 40 landmark object images. Target stimuli were a subset of object images used by Brady et al. (2013), which were colour-rotated in 360° CIELAB perceptually uniform colour space (International Organization for Standardization, 2019) to randomly vary their hue at study and test (see Figure 2 for an example of a colour-rotated target stimulus). The CIELAB colour space is well suited for continuous manipulations of colour as a given distance between two colours in this space approximates their perceptual colour distance. This property of the CIELAB colour space has previously been leveraged to investigate the fidelity of both working memory (e.g., Bays, Catalao, & Husain, 2009; Zhang & Luck, 2008; Panichello et al., 2019) and long-term memory (e.g., Brady et al., 2013; Korkki et al., 2020; Richter et al., 2016). However, to minimise potential biases in colour memory, only objects without specific colour associations were selected for

use as target stimuli this study. By contrast, landmark stimuli, which represented natural and manmade environmental features, were identical to those used in the previous study.

Additionally, both targets and landmarks had the same pixel resolution and dimensions in virtual meters (vm) as in the previous study. These stimuli were likewise presented as view plane-aligned 2D sprites to equate the amount of perceptual information associated with each object, regardless of vantage point.



Figure 2. An example target object stimulus, colour-rotated in 60° increments. Note that colour hue was allowed to vary continuously during the actual experiment.

Procedure

In a mixed design, aphantasic and control participants completed a novel computer-based 3D object and spatial memory task and two questionnaires relating to mental imagery and memory experience. Both the memory task and questionnaires were completed in a single online testing session, and their order was counterbalanced across participants. The memory task presented in this chapter was based on the task used in the previous study and closely followed its procedure (for details, see the Methods section of Chapter 3), except for the test phase. To recapitulate, the main task consisted of 10 testing blocks, with each comprising an exploration, study, arithmetic, and test phase. In the exploration phase, participants familiarised themselves with the circular testing environment from both first-person and third-person perspectives. The testing environment changed with every block and was differentiated by four unique external landmarks placed in cardinal directions just beyond the boundary wall. Importantly, these landmarks aided locational memory and served as stable orientation cues when in first person. Next, in the study phase, participants learned the colour and location (relative to the landmarks) of eight target objects. These target objects were presented in a sequence at random locations within the testing environment. Participants then solved self-paced simple arithmetic problems for 30s to prevent working memory rehearsal before finally beginning the test phase (see Figure 3 on next page for schematic illustration of the task).

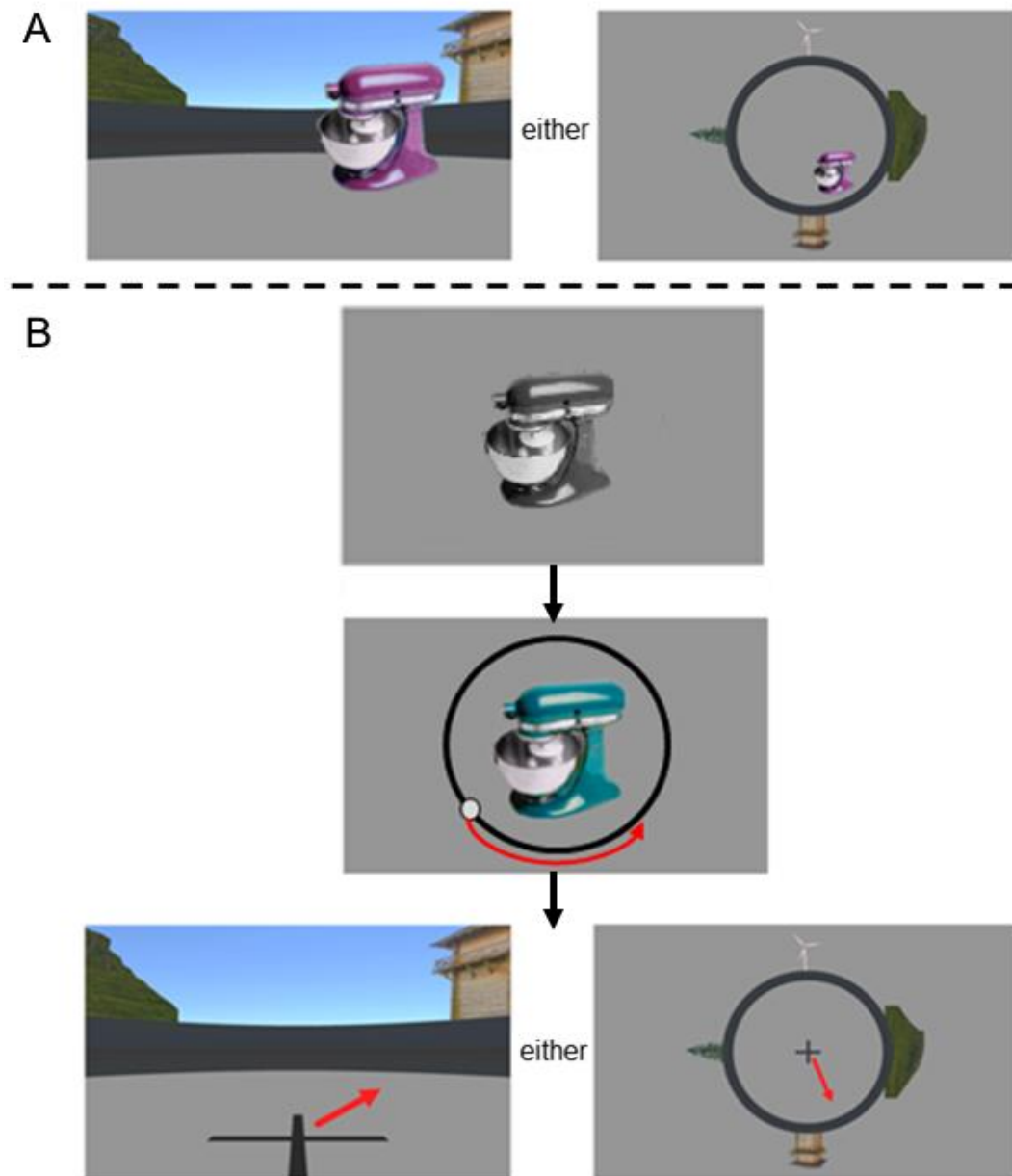


Figure 3. Schematic representation of a testing block in the object and spatial memory task.

Participants initially familiarised themselves with the testing environment during the exploration phase (not shown). A) Then, in the study phase, participants learned the colour and location of eight target objects. These target objects were presented in a series at random locations in the testing environment, which were viewed from either a first-person (left) or third-person (right) perspective. After the study phase, participants solved simple self-paced arithmetic problems for 30s (not shown). B) Finally, in the test phase, studied target objects were first cued (top) before participants made subjective memory imagery vividness ratings on (not shown), then reproduced, their object (middle) and spatial memory features, the latter of which were tested in the same or alternative studied perspective (bottom left or right). Vividness ratings always preceded feature reproduction, but object and spatial memory assessment order randomly varied. Note that target object size has been increased for clarity in this figure.

The test phase of the present task differed significantly from that of the previous study. In the test phase, participants rated the vividness of, and reproduced, both the colour (i.e., object memory) and location (i.e., spatial memory) of the eight target objects studied earlier in the block. No unstudied objects were tested. This resulted in a total of 80 test trials in the main task. These trials were equally split across first person and third person perspective conditions in the object memory assessment (i.e., 40 target object colours were studied in first-person and 40 in third-person), which were further divided into perspective switch and stay conditions in the spatial memory assessment (i.e., 20 target object locations were studied and tested in first person, 20 were studied in third person but tested in first person, 20 were studied and tested in third person, and 20 were studied in first person but tested in third person). Furthermore, these conditions were pseudorandomly allocated to each test phase in equal proportions. All test trials began with the presentation of a black central fixation cross for 500ms. This was followed by the cueing of a studied object in greyscale for 1s., then the object and spatial memory assessments. Both feature assessments were separated by a 500ms-long black central fixation cross and their order was randomised across trials. However, the vividness of both memory features was assessed before feature reproduction. This was done to eliminate the influence of memory performance on subjective vividness ratings (Richter et al., 2016).

Object memory. The object memory assessment was adapted from the continuous report task developed by Richter et al. (2016). First, participants rated the subjective vividness with which they could remember a cued target object's studied colour. To increase the likelihood that these task-based vividness ratings would tap the same construct of mental imagery as the VVIQ, the same language was used to define the ratings scale. These ratings could span a continuum ranging from 0 (i.e., "no imagery at all" for colour) to 100 (i.e., colour imagery "as vivid as sight") and were made using a horizontal response slider. Participants indicated the level of colour vividness by holding the 'a' or 'd' keyboard keys to move the slider left or right. Both the ratings slider and this scale remained on-screen until participants made a response by pressing the 'space' key or the 10s deadline was reached. Following the vividness rating, participants had up to 15 seconds to reproduce the studied colour hue of the cued target object as precisely as they could from memory. The target object remained on-screen during this period and was initially presented in a random hue that differed from its original. Participants adjusted the colour hue of the target object by holding the 'a' or 'd' keys to move a response slider that encircled the target clockwise or counter-

clockwise. As with the vividness rating, participants submitted their response by pressing the ‘space’ key.

Spatial memory. Participants first rated the vividness with which they could remember a cued target object within the greater scene. Like the object memory assessment, these ratings were made using the same continuous scale, response slider, and controls and within the same 10s response deadline. Similarly, participants then had up to 15s to precisely reproduce the target object’s studied location from memory. This (objective) part of the spatial memory assessment was identical to the test phase of the previous study (see Chapter 3 for details). Briefly, the testing environment in which these responses were made was viewed from either the same (i.e., perspective stay condition) or alternative (i.e., perspective switch condition) studied perspective of the target object. At the start of this period, participants were placed in the environment’s centre and faced a random direction when in first person whereas the camera was placed at fixed height facing down toward the ground when in third person. Viewpoint could be adjusted in both conditions by rotating the first-person camera left/right or zooming the third-person camera in/out using the computer mouse/trackpad. Participants pressed the ‘w’, ‘a’, ‘s’, and ‘d’ keys to move a black crosshair, placed on the ground ahead of the first-person camera or centred under third-person camera, to precisely indicate a given target object’s studied location. Responses were submitted by pressing the ‘space’ key.

Questionnaires

Measures of general mental imagery and memory experience were obtained for each participant using the VVIQ and the Survey of Autobiographical Memory (SAM; Palombo et al., 2013) self-report questionnaires, respectively. The VVIQ consists of 16 items to which participants rate their level of agreement with statements related to person and scene visual mental imagery. VVIQ items are rated using a 5-point Likert scale, with ratings of 1 corresponding to “no image at all, you only ‘know’ that you are thinking of the object” while ratings of 5 correspond to imagery “perfectly clear and as vivid as normal vision”. VVIQ scores range from 16 to 80. The SAM has 26 items and measures agreement level with statements related to various memory abilities. Like the VVIQ, SAM items are rated using a 5-point scale, with a score of 1 corresponding to “strongly disagree” while a score of 5 corresponds to “strongly agree”. The total SAM score, as well as separate scores for the episodic, semantic, spatial, and future subcomponents, were derived from item-specific weights for each response using materials provided by the questionnaire’s creators.

Task measures and analysis

The main analysis was performed on mean object and spatial memory performance and their corresponding imagery vividness ratings. Raw object memory errors were quantified as the absolute angular deviation between a given target object's studied colour hue and the hue reproduced by a participant (range = 0-180°). However, raw errors on continuous report tasks like the one used here to probe object memory are thought to reflect both the overall success and varying precision of episodic memory retrieval, properties that have been separated behaviourally (Harlow & Yonelinas, 2016) and neurally (Richter et al., 2016) using probabilistic mixture modelling (Bays et al., 2009; Zhang & Luck, 2008).

Given that a measure of the precision of object memory retrieval rather than its overall success is more likely to be sensitive to mental imagery-based deficits, which might otherwise be compensated for using alternative (e.g., verbal) strategies (Keogh, Wicken, & Pearson, 2021), a mixture model was fitted to the raw object memory errors for each task condition and in each participant. These mixture models had two components: a von Mises circular normal distribution centred at a mean raw error of 0°, with a concentration parameter Kappa (K), and a circular uniform distribution representing the probability of random guesses (pU). Retrieval success (pT) was calculated as the probability of responses emanating from the von Mises distribution versus the uniform distribution ($pT = 1 - pU$), whereas retrieval precision (K) was the concentration of the von Mises distribution. pT ranged from 0 (i.e., complete retrieval failure) to 1 (i.e., complete retrieval success), with 0.5 reflecting random guesses. By contrast, K had a minimum value of 0, reflecting a perfectly uniform response distribution, with increasing values indicating increasing levels of object memory precision.

As in the previous study, raw spatial memory errors reflecting the Euclidean distance between a given target object's studied location and the location indicated by a participant were converted to memory scores (MS), which correct for location-specific differences in difficulty (for details on this computation, see the Methods section of Chapter 3). MS ranges from 0 (i.e., worst possible performance) to 1 (i.e., perfect performance), with 0.5 corresponding to chance-level performance. Median response time (RT) was also examined for both object and spatial memory task components. As in Chapter 3, trials in which no responses were given or given within 500ms were excluded from analysis (5% of all trials in control participants and 6% of all trials in aphantasic participants in the present study).

All analyses were conducted using R Statistical Software (v4.1.2; R Foundation for Statistical Computing, Vienna, Austria). Linear mixed models were run on mean object and spatial memory vividness ratings and performance measures using the ‘lme4’ package (Bates et al., 2015). All models were fitted via restricted maximum likelihood parameter estimation and all models included the between-subjects fixed factor of *imagery group* (controls, aphantasics). However, these models differed in their number of within-subjects fixed factors. The object memory model had a single within-subjects fixed factor of *study perspective* (first person, third person), representing the perspective in which a given object feature was studied and tested. As visual perspective was additionally manipulated in the spatial memory component of the task during the test phase, the corresponding model had two within-subjects fixed factors of *switch status* (stay, switch) and *test perspective* (first person, third person). These fixed factors were represented using effects coding as their interactions were of chief concern (Singmann & Kellen, 2019). Under this scheme, fixed factor coefficients indicate the deviation of each factor level from the grand mean, represented by the intercept. Finally, all models accounted for repeated measures by including a by-subject random intercept (Barr, 2013; Barr et al., 2013). The general form of the object (1) and spatial (2) memory models are provided below in lme4 syntax:

```
object ~ imageryGroup * studyPerspective + (1 | subject) (1)
```

```
spatial ~ imageryGroup * switchStatus * testPerspective + (1 | subject) (2)
```

Model assumptions were evaluated by inspecting standard diagnostic residual plots. Outliers were detected using the interquartile range method (i.e., values greater than 1.5x the interquartile range). The influence of outliers, where present, was checked by re-running analyses without the subjects who contributed them. As in the previous chapter, *p*-values for the fixed effects were calculated using Satterthwaite degrees of freedom approximation (Satterthwaite, 1941), implemented in the ‘lmerTest’ package (Kuznetsova, Brockhoff, & Christensen, 2017). Significant interactions were followed up on with simple contrasts on the estimated marginal means using the “modelbased” package (Makowski et al., 2020). All tests were two-sided and used a canonical alpha level of 0.05. Exact *p*-values are reported to three decimal places (unless $p < 0.001$).

Results

Demographics and questionnaires

Demographics. Due to unequal sample sizes, a Welch's two-sample *t*-test assuming unequal between-group variances was conducted on age and found no significant difference between aphantasic and non-aphantasic participants ($t(42.94) = 0.66, p = 0.514$). These groups did not significantly differ in the proportion of males and females as determined by a Fisher's exact test of independence on the sex count data ($p = 0.551$, *Fisher's exact test*). A Mann-Whitney U test was performed on formal education level and similarly found no significant between-group difference ($W = 304, p = 0.295$). Together, these results indicate aphantasic and control groups were matched on all demographic variables (see Table 1 for descriptive statistics).

Table 1. Mean (SD in brackets) participant demographic and questionnaire data.

Variable	Controls ($n = 27$)	Aphantasics ($n = 20$)	<i>p</i> -value
Age	27.73 (5.60)	26.70 (5.01)	0.514 ^a
Sex	12 male, 15 female	7 male, 13 female	0.551 ^b
Education	undergraduate	undergraduate	0.295 ^c
VVIQ	51.37 (11.20)	17.70 (3.18)	< 0.001 ^a
SAM	93.83 (12.28)	84.90 (12.71)	0.020 ^a
Episodic	99.62 (13.75)	86.69 (13.01)	0.002 ^a
Semantic	95.12 (13.70)	97.45 (17.90)	0.630 ^a
Spatial	90.70 (18.08)	87.49 (18.56)	0.557 ^a
Future	90.81 (10.75)	79.43 (2.33)	< 0.001 ^a

Note. VVIQ = Vividness of Visual Imagery Questionnaire, SAM = Survey of Autobiographical Memory. The median education level is reported.

a Tested using a two-sided Welch's two-sample *t*-test.

b Tested using a two-sided Fisher's exact test of independence.

c Tested using a two-sided Mann-Whitney U test.

Questionnaires. Welch's two-sample *t*-tests assuming unequal between-group variances were performed on the VVIQ, SAM composite, and SAM component scores (see Table 1). On the VVIQ, aphantasic participants reported significantly less vivid visual mental imagery than controls ($t(31.46) = 14.83, p < 0.001$). Aphantasic participants also reported significantly worse overall memory ability than controls, as measured by the SAM composite score ($t(40.29) = 2.42, p = 0.020$). Consistent with a selective deficit in episodic cognition, however, aphantasics reported significantly lower ability in episodic memory ($t(42.27) =$

3.29, $p = 0.002$) and future event prospection ($t(29.25) = 5.33$, $p < 0.001$), but not in semantic memory ($t(34.34) = -0.49$, $p = 0.630$) or spatial memory ($t(40.48) = 0.59$, $p = 0.557$).

Object memory

Vividness. The model on object memory vividness (Figure 4A) had a significant intercept ($\beta = 48.53$, $SE = 3.58$, $t(45) = 13.56$, $p < 0.001$). As predicted, there was a significant main effect of *imagery group* ($\beta = 14.07$, $SE = 3.58$, $t(45) = 3.93$, $p < 0.001$), where aphantasic participants rated their object memory vividness lower than controls (see Table 2 for descriptive statistics). There was no significant main effect of *study perspective* ($\beta = 0.39$, $SE = 0.36$, $t(45) = 1.08$, $p = 0.285$) or a significant *imagery group* x *study perspective* interaction ($\beta = -0.10$, $SE = 0.36$, $t(45) = -0.28$, $p = 0.784$). No outliers were detected in these data. For descriptive statistics of the vividness ratings and performance measures on the object memory component of task, see Table 2 below.

Table 2. Mean (*SD in brackets*) object memory vividness and performance measures.

Condition	Controls				Aphantasics			
	Vividness	pT	K	RT	Vividness	pT	K	RT
First person	62.89	0.81	11.09	4.72	34.95	0.83	11.25	5.00
	(15.30)	(0.13)	(7.70)	(1.13)	(32.94)	(0.15)	(5.14)	(1.37)
Third person	62.31	0.82	8.11	5.01	33.98	0.80	8.73	5.38
	(15.68)	(0.13)	(5.19)	(1.32)	(32.80)	(0.21)	(4.55)	(1.36)

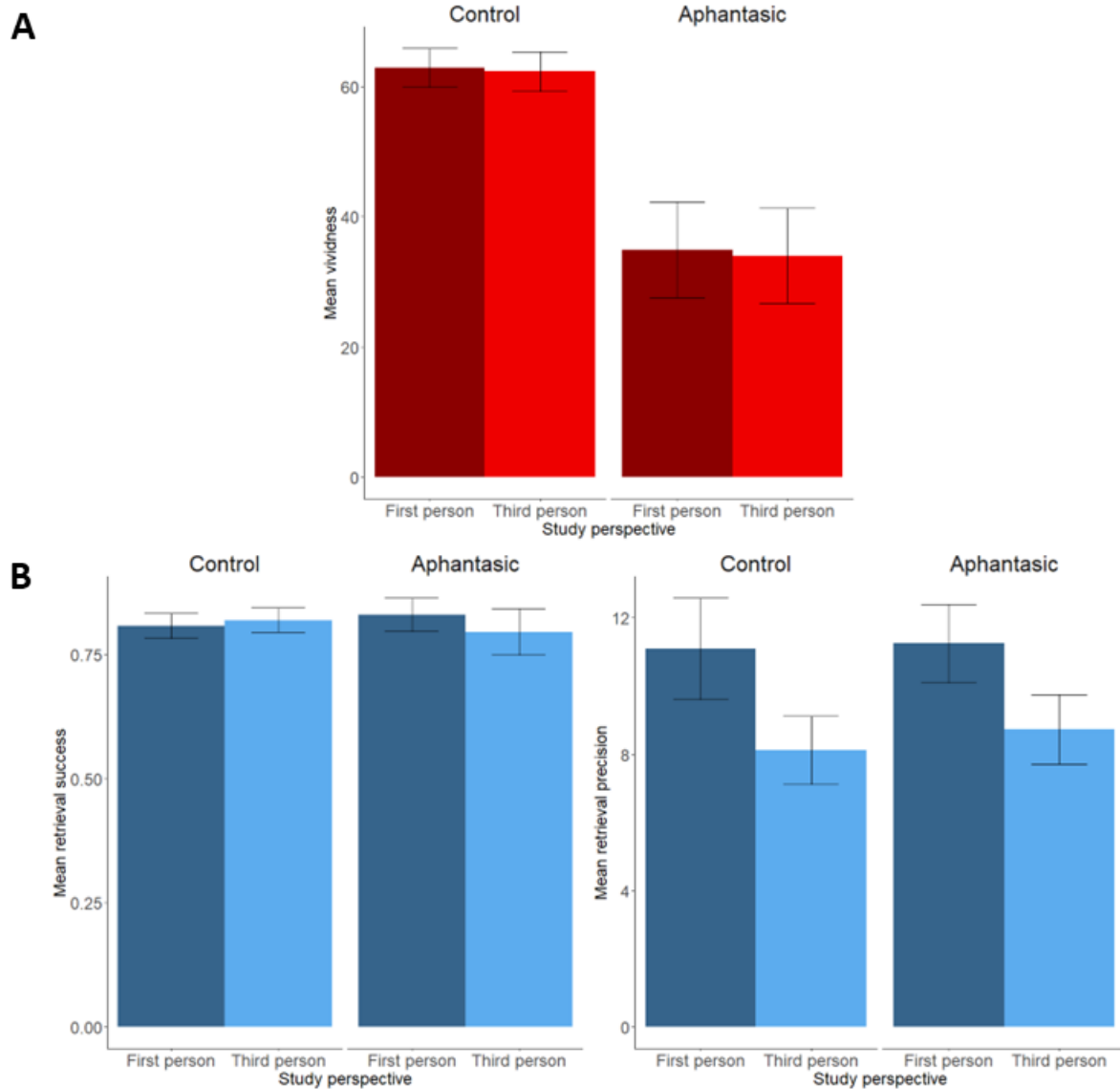


Figure 4. Mean object memory vividness ratings (A) and retrieval success (B, left) and precision (B, right) measures across imagery groups and task perspective conditions. Error bars denote SEM.

Retrieval success. The model on object memory retrieval success (see Figure 5B, left) had a significant intercept ($\beta = 0.81$, $SE = 0.02$, $t(45) = 39.34$, $p < 0.001$). There were no significant main effects of *imagery group* ($\beta < 0.01$, $SE = 0.02$, $t(45) = 0.02$, $p = 0.980$) or *study perspective* ($\beta < 0.01$, $SE < 0.01$, $t(45) = 0.62$, $p = 0.540$). Likewise, there was no significant *imagery group* $\times$ *study perspective* interaction ($\beta < -0.01$, $SE < 0.01$, $t(45) = -1.20$, $p = 0.230$). One outlier participant was detected, but their exclusion did not influence the results.

Retrieval precision. The model on object memory precision (see Figure 3B, right) had a significant intercept ($\beta = 9.80$, $SE = 0.76$, $t(45) = 12.87$, $p < 0.001$). Contrary to my prediction, there was no significant main effect of *imagery group* ($\beta = -0.20$, $SE = 0.76$, $t(45)$

= -0.26, $p = 0.797$). However, there was a significant main effect of *study perspective* ($\beta = 1.38$, $SE = 0.42$, $t(45) = 3.24$, $p = 0.002$), where object memory was generally recalled with higher fidelity when studied in a first-person versus a third-person perspective (see Table 2). There was no significant *imagery group* x *study perspective* interaction ($\beta = 0.12$, $SE = 0.42$, $t(45) = 0.27$, $p = 0.787$). Excluding outlier participants ($n = 5$) did not affect the results.

Raw error. For completeness, raw object memory errors, which were not derived from mixture modelling, were also analysed. This model had a significant intercept ($\beta = 30.35$, $SE = 1.71$, $t(45) = 17.72$, $p < 0.001$). Mirroring the analyses of pT and K , there was a significant main effect of *study perspective* ($\beta = -1.72$, $SE = 0.63$, $t(45) = -2.71$, $p = 0.010$), but no significant main effect of *imagery group* ($\beta = 1.12$, $SE = 1.71$, $t(45) = 0.66$, $p = 0.516$) or a significant *imagery group* x *study perspective* interaction ($\beta = 0.645$, $SE = 0.63$, $t(45) = 1.02$, $p = 0.314$), suggesting the lack of group differences in object memory retrieval success and precision were unlikely to be attributable to the modelling approach used to derive those measures. One outlier participant was excluded, but the results did not change.

Response time. Finally, the model on object memory RTs (see Table 2) had a significant intercept ($\beta = 5.03$, $SE = 0.19$, $t(45) = 27.08$, $p < 0.001$). There was no significant main effect of *imagery group* ($\beta = -0.16$, $SE = 0.19$, $t(45) = -0.88$, $p = 0.390$), but there was a significant main effect of *study perspective* ($\beta = -0.16$, $SE = 0.04$, $t(45) = -4.19$, $p < 0.001$). The *imagery group* x *study perspective* interaction was not significant ($\beta = 0.02$, $SE = 0.04$, $t(45) = 0.59$, $p = 0.558$). Two outlier participants were detected, but their removal did not change the results.

Spatial memory

Vividness. The model on spatial memory vividness (see Figure 4A) had a significant intercept ($\beta = 38.32$, $SE = 3.24$, $t(45) = 11.83$, $p < 0.001$). As in the object memory analysis, there was a significant main effect of *imagery group* ($\beta = 12.93$, $SE = 3.24$, $t(45) = 3.99$, $p < 0.001$), where aphantasic participants rated their spatial memory vividness lower than controls. There were no significant main effects of *switch status* ($\beta = -0.37$, $SE = 0.49$, $t(135) = -0.76$, $p = 0.447$) or *test perspective* ($\beta = 0.06$, $SE = 0.49$, $t(135) = 0.13$, $p = 0.899$). There was, however, a significant *switch status* x *test perspective* interaction ($\beta = -1.55$, $SE = 0.49$, $t(135) = -3.18$, $p = 0.002$), but no significant *imagery group* x *switch status* ($\beta = 0.35$, $SE = 0.49$, $t(135) = 0.71$, $p = 0.477$) or *imagery group* x *test perspective* ($\beta = -0.04$, $SE = 0.49$, $t(135) = -0.09$, $p = 0.931$) interactions. Finally, the *imagery group* x *switch status* x *test*

perspective interaction was significant ($\beta = -1.28$, $SE = 0.49$, $t(135) = -2.63$, $p = 0.010$).

Excluding outlier participants ($n = 3$) did not change the pattern of results. See Table 3 below for descriptive statistics of all spatial memory measures.

Table 3. Mean (SD in brackets) spatial memory vividness and performance measures.

Condition	Controls			Aphantasics		
	Vividness	MS	RT	Vividness	MS	RT
First person						
Stay	47.86 (15.63)	0.75 (0.09)	5.31 (1.51)	25.44 (27.18)	0.77 (0.11)	5.03 (1.60)
Switch	52.50 (18.91)	0.78 (0.13)	5.53 (1.72)	28.10 (29.53)	0.81 (0.11)	5.16 (1.76)
Third person						
Stay	52.65 (19.64)	0.85 (0.10)	4.06 (1.79)	26.26 (27.92)	0.85 (0.12)	3.64 (1.46)
Switch	47.29 (16.32)	0.76 (0.09)	4.16 (1.88)	26.83 (27.20)	0.78 (0.11)	3.64 (1.30)

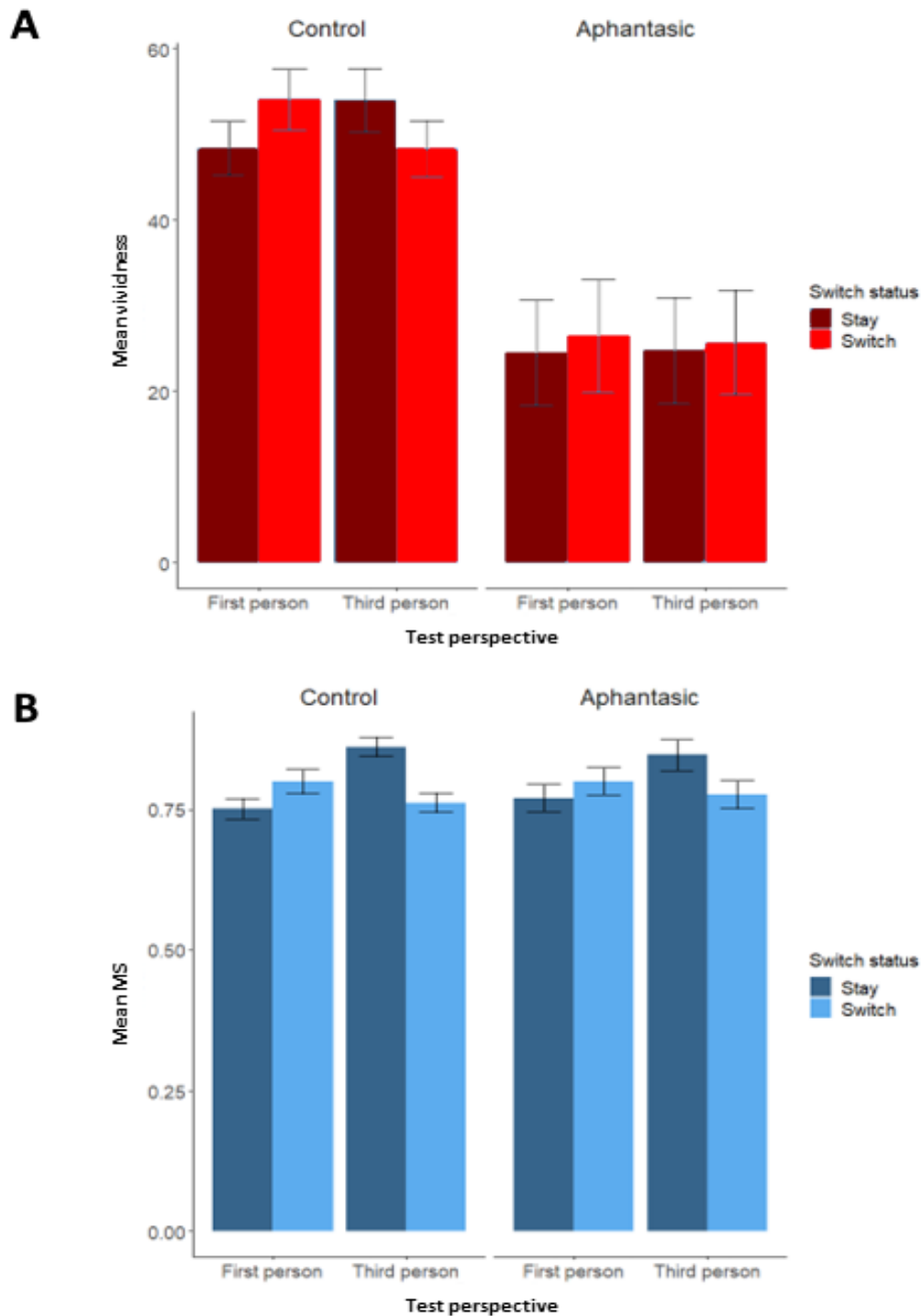


Figure 5. Mean spatial memory vividness ratings (A) and MS (B) across imager groups and switch status and test perspective task conditions. Error bars denote SEM.

To decompose the significant three-way interaction in the analysis of spatial memory vividness, the simple effects of *imagery group*, conditioned on *switch status* x *test perspective*, were initially investigated. Relative to the aphantasic participants, control participants had significantly higher vividness ratings in both stay first person ($\beta = 30.30$, SE

= 6.72, $t(46) = 4.50$, $p < 0.001$) and switch first person ($\beta = 34.90$, $SE = 6.72$, $t(46) = 5.19$, $p < 0.001$) trials. Likewise, control participants rated their vividness significantly higher than aphantasics in both stay third person trials ($\beta = 34.70$, $SE = 6.72$, $t(46) = 5.16$, $p < 0.001$) and switch third person trials ($\beta = 28.9$, $SE = 6.72$, $t(46) = 45.80$, $p < 0.001$).

The simple effects of *test perspective*, conditioned on *imagery group* and *switch status*, were then examined. Stay first person vividness ratings were significantly lower than stay third person vividness ratings in control participants ($\beta = -5.63$, $SE = 1.88$, $t(114) = -2.99$, $p = 0.003$) but not aphantasic participants ($\beta = -1.20$, $SE = 2.71$, $t(114) = -0.44$, $p = 0.660$). In comparison, switch first person vividness ratings were significantly higher than switch third person vividness ratings in control participants ($\beta = 5.71$, $SE = 1.88$, $t(114) = 3.03$, $p = 0.003$) but not aphantasic participants ($\beta = -0.26$, $SE = 2.71$, $t(114) = -0.10$, $p = 0.924$).

Finally, the simple effects of *switch status*, conditioned on *imagery group* and *test perspective*. Vividness ratings in stay first person trials were significantly lower than in switch first person trials in control participants ($\beta = -5.71$, $SE = 1.88$, $t(114) = -3.04$, $p < 0.003$), whereas this difference was not significant in aphantasic participants ($\beta = -11.11$, $SE = 2.71$, $t(114) = -0.410$, $p = 0.683$). In contrast, stay third person vividness ratings were significantly higher than switch third person vividness ratings in control participants ($\beta = 5.62$, $SE = 1.88$, $t(114) = 2.99$, $p = 0.003$) but not in aphantasic participants ($\beta = -0.17$, $SE = 2.71$, $t(114) = -0.06$, $p = 0.949$). Considering the results of the simple effects analyses together, a crossover interaction is apparent in the control group but not the aphantasic group. More specifically, spatial memory vividness is higher in those with typical imagery when object locations are studied in third person versus first person, irrespective of the test perspective. On the other hand, those with atypical imagery have lower spatial memory vividness in general.

Memory score. The model on spatial memory score (see Figure 4B) had a significant intercept ($\beta = 0.80$, $SE = 0.01$, $t(45) = 63.85$, $p < 0.001$). There were significant main effects of *switch status* ($\beta = 0.01$, $SE < 0.01$, $t(135) = -3.13$, $p = 0.024$) and *test perspective* ($\beta = -0.02$, $SE < 0.01$, $t(135) = -3.13$, $p = 0.002$), but not *imagery group* ($\beta < -0.01$, $SE = 0.01$, $t(45) = -0.20$, $p = 0.845$). There was a significant *switch status* x *test perspective* interaction ($\beta = -0.03$, $SE < 0.01$, $t(135) = -6.19$, $p < 0.001$) but not *imagery group* x *switch status* ($\beta < 0.01$, $SE < 0.01$, $t(135) = 0.28$, $p = 0.781$) or *imagery group* x *test perspective* ($\beta < -0.01$, $SE <$

0.01, $t(135) = -0.49$, $p = 0.624$). The *imagery group* $\times$ *switch status* $\times$ *test perspective* interaction was not significant ($\beta < 0.01$, $SE < 0.01$, $t(135) = -1.18$, $p = 0.240$). Excluding outlier participants ($n = 2$) did not influence the results.

The significant *switch status* $\times$ *test perspective* interaction in the analysis of spatial memory score was decomposed by examining the simple effects of *test perspective*, conditioned on *switch status*, and averaged over *imagery group*. As predicted, stay first person MS was significantly lower than stay third person MS ($\beta = -0.09$, $SE = 0.01$, $t(135) = -6.59$, $p < 0.001$), suggesting that spatial memory accuracy is generally less accurate when studied and tested in first person versus third person. In comparison, however, switch first person MS was significantly higher than switch third person MS ($\beta = 0.03$, $SE = 0.01$, $t(135) = 2.16$, $p = 0.032$). Together, these results indicate that a third person perspective, whether encoded as such or adopted during subsequent retrieval, enhances spatial memory accuracy.

Response time. Lastly, the model on spatial memory RTs (see Table 3) had a significant intercept ($\beta = 4.65$, $SE = 0.22$, $t(45) = 21.41$, $p < 0.001$). The main effect of *imagery group* was not significant ($\beta = 0.26$, $SE = 0.22$, $t(45) = 1.21$, $p = 0.230$) but the main effect of *test perspective* was ($\beta = 0.73$, $SE = 0.5$, $t(135) = 13.50$, $p < 0.001$). There was no significant main effect of *switch status* ($\beta = -0.07$, $SE = 0.05$, $t(135) = -1.21$, $p = 0.23$), nor were there significant interactions of *switch status* $\times$ *test perspective* ($\beta = -0.4$, $SE = 0.05$, $t(135) = -0.74$, $p = 0.46$), *imagery group* $\times$ *switch status* ($\beta = -0.02$, $SE = 0.05$, $t(135) = -0.37$, $p = 0.71$), *imagery group* $\times$ *test perspective* ($\beta = -0.02$, $SE = 0.05$, $t(135) = -0.37$, $p = 0.71$), or *imagery group* $\times$ *switch status* $\times$ *test perspective* ($\beta = -0.02$, $SE = 0.05$, $t(135) = -0.38$, $p = 0.71$). Three outlier participants were detected, but their exclusion did not affect results.

Influence of mental imagery vividness criteria on task performance

The main analysis was re-run under two alternative VVIQ cut-off(s) to explore whether the degree of self-rated imagery experience influenced the results. While the aphantasic participants in the present study had a mean VVIQ of 17.70, which is near the floor score of 16 as expected, only those reporting a complete absence of mental imagery were included in the aphantasic group for the first re-analysis. Accordingly, $n = 7$ aphantasics were excluded ($VVIQ > 16$), but no significant main effect of, or interaction with, *imagery group* was revealed (all $ps \geq 0.190$). In contrast to the aphantasic participants, control participants had a mean VVIQ of 51.37, which is notably lower than the population mean VVIQ of 59.20 as suggested by a meta-analysis (McKelvie, 1995). Therefore, the absence of

any group memory differences may instead be attributable to below average mental imagery experience in the control group. To address this possibility, all participants were re-classified according to the stricter cut-off scores of Bainbridge et al. (2021), who found object but not spatial memory deficits in their aphantasic participants. This resulted in the exclusion of $n = 1$ aphantasic participant ($VVIQ > 25$) and $n = 5$ control participants ($VVIQ < 40$). No significant group differences emerged in this analysis either (all $ps \geq 0.337$).

As $n = 9$ aphantasic participants had mean task-based object and/or spatial memory vividness ratings near the floor (vividness < 10), the main analysis was also re-run with only these participants included in the aphantasic group. No significant group differences were revealed in the re-analysis of model-derived object memory retrieval success or precision measures (all $ps \geq 0.400$). Additionally, in the re-analysis of raw object memory errors, the main effect of *imagery group* did not reach significance ($\beta = 2.92$, $SE = 1.84$, $t(36) = -15.56$, $p = 0.120$), but control participants unexpectedly had numerically greater raw object memory error than aphantasic participants. Neither the main effect of *study perspective* nor *imagery group* $\times$ *study perspective* interaction was significant in this analysis (both $ps \geq 0.190$). Likewise, in the re-analysis of spatial memory performance, the overall pattern of results concerning the main effect of *imagery group* or interactions with this factor did not change (all $ps \geq 0.560$).

Relationship between subjective and objective memory measures

As indicated by the apparent lack of agreement between task-based subjective vividness ratings and objective performance in the aphantasic participants, a subset of those people with aphantasia might have a deficit in meta-cognitive awareness of mental imagery rather than in imagery itself (Pounder et al., 2022). To explore this possibility in the present data, correlations were run within groups on the memory task vividness ratings and performance measures to see whether their assumed relationship in control participants is reduced or absent in aphantasic participants. Standard Pearson correlations were run in the control group. By contrast, rank-based Kendall's correlations were run in the aphantasic group to account for floor effects in their VVIQ scores and task-based vividness ratings. The number of tests was reduced by averaging across task conditions to obtain single measures of object and spatial memory vividness and performance. As the pattern of results in the main analysis of the object memory component of the task did not depend on the measure used (i.e., raw error, retrieval success, and retrieval precision), object memory performance was

quantified here with the raw errors to further reduce the number of tests. By contrast, spatial memory performance remained characterised by MS.

First, the correlation between VVIQ score and task-based memory vividness ratings was checked to see whether these measures tapped the same construct of mental imagery. This relationship was not significant in the control participants for object memory ($r(25) = 0.36$, $p = 0.070$) but was significant for spatial memory ($r(25) = 0.58$, $p = 0.001$). In the aphantasic participants, there was no significant relationship between VVIQ score and the vividness of object memory ($r_b = 0.15$, $p = 0.420$) or spatial memory ($r_b = 0.26$, $p = 0.160$), suggesting the aphantasic participants might have interpreted the VVIQ and task-based vividness ratings as measuring different constructs.

Next, the correlation between vividness ratings and performance in the memory task was examined. In the control participants, this relationship was significant and in the expected direction for both object memory ($r(25) = -0.73$, $p = < 0.001$; see Figure 6, top left) and spatial memory ($r(25) = 0.52$, $p = 0.006$; see Figure 5, bottom left). In the aphantasic participants, the correlation between vividness ratings and performance was not significant for object memory ($r_b = -0.09$, $p = 0.580$; see Figure 5, top right), and failed to reach significance for spatial memory ($r_b = 0.26$, $p = 0.110$; see Figure 6, bottom right).

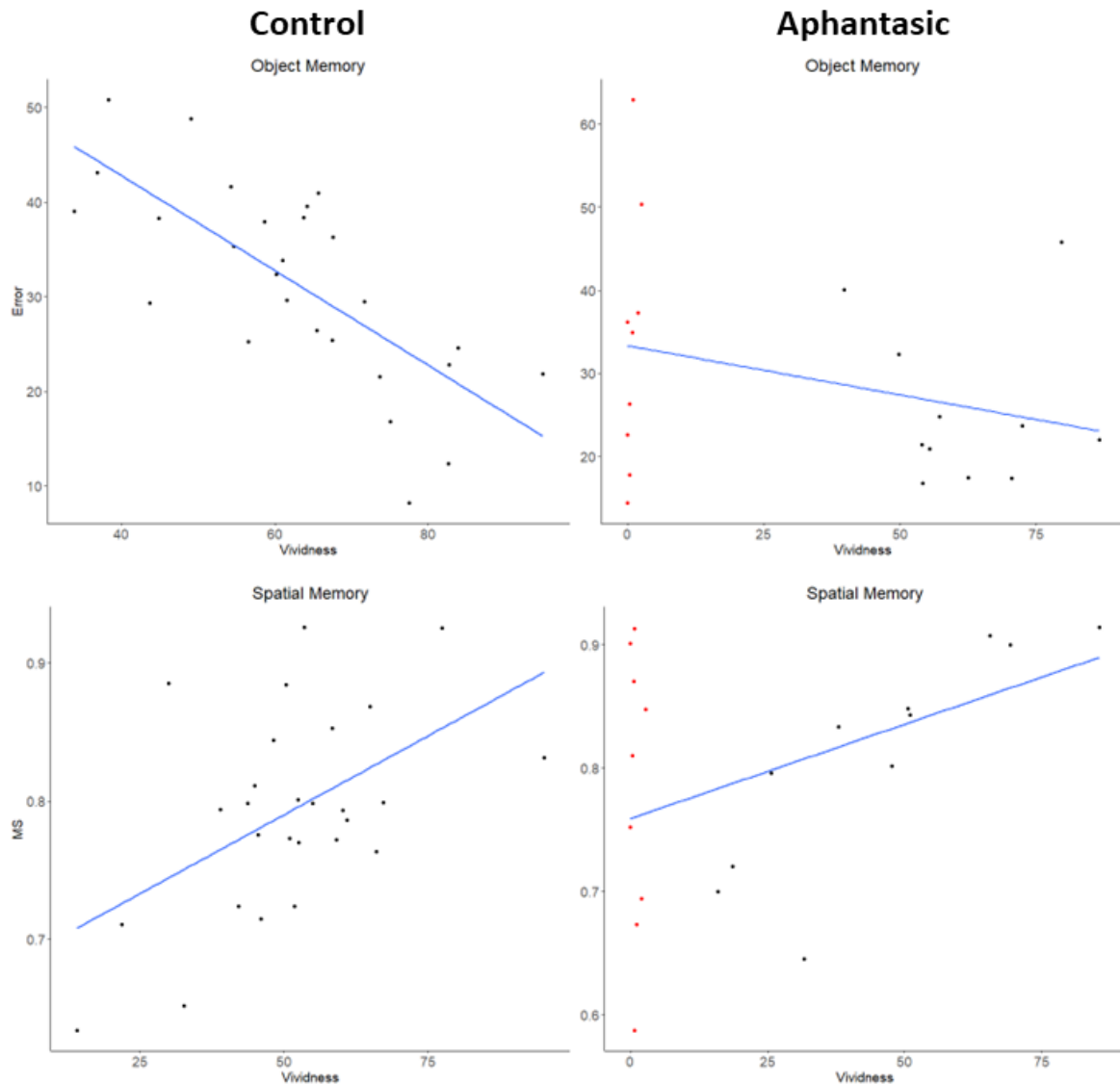


Figure 6. Plots showing the relationship between mean vividness ratings and performance for object (top) and spatial (bottom) memory features in control (left) and aphantasic participants (right). Red-highlighted datapoints denote the subgroup of aphantasic participants who rated their task-based memory vividness at floor.

As the correlations between overall object and spatial memory vividness ratings and performance were significant in the control participants (see Figure 6, left), these relationships were further broken down in this group by visual perspective. These relationships were significant for object features studied both in first person ($r(25) = -0.79, p < 0.001$) and in third person ($r(25) = -0.60, p = 0.001$). All but the stay first-person condition of the spatial memory component of the task were significant (stay first person: $r(25) = 0.25, p = 0.200$; switch first person: $r(25) = 0.64, p < 0.001$; stay third person $r(25) = 0.57, p = 0.002$; switch third person: $r(25) = 0.60, p = 0.001$).

Finally, two distinct clusters were evident in the aphantasic correlation plots (see Figure 6, right), with one subgroup ($n = 9$) rating their memory vividness at floor (vividness < 10) despite wide ranging performance and another subgroup ($n = 11$) rating their memory vividness and performance ostensibly more in line with controls. Additionally, it should be noted that those who rated their memory vividness for object features at floor did so too for spatial features. Further correlations were run in the latter aphantasic subgroup, which remained non-significant for object memory ($r_b = -0.09, p = 0.800$), but became significant for spatial memory ($r_b = 0.78, p < 0.005$). The relationship in this subgroup between VVIQ and object memory vividness ratings stayed non-significant ($r_b = -0.09, p = 0.700$) as did the relationship between VVIQ and spatial memory vividness ratings ($r_b = -0.26, p = 0.300$).

Discussion

This study investigated whether first-person (egocentric) episodic recall is more impaired than third-person (allocentric) episodic recall in people with aphantasia. To this end, a novel 3D object and spatial memory task was employed to assess the effects of visual and spatial imagery abilities in self-identified aphantasics on subjective and objective measures of episodic memory. Aphantasic participants showed no deficits in object or spatial memory performance, despite rating the vividness of both memory features lower than controls. Moreover, aphantasic participants did not differ from controls in their ability to manipulate visuospatial representations as indicated by the comparable levels of switch versus stay trial performance in both groups. Further exploratory correlation analysis revealed a relationship between task performance and imagery vividness in the control participants but not in the aphantasic participants. Together, these results suggest that some aphantasics might have a deficit in meta-cognitive awareness of mental imagery rather than in imagery itself.

Contrary to my necessarily speculative predictions given the limited prior literature, there were no differences between aphantasic and control participants in object or spatial memory performance. The apparent lack of an object memory deficit in the current aphantasic participants is noteworthy given previous subjective self-reports of selective object imagery deficits (Dawes et al., 2020; Dawes et al., 2022) and recent work by Bainbridge et al. (2021), who showed object memory to be objectively impaired in aphantasics, who were tasked with drawing 2D photographs of scenes from memory. Importantly, Bainbridge et al. (2021) ruled out group differences in perceptual or drawing abilities as a confound, as their aphantasic participants performed normally on the copy drawing version of their task. Sex differences in colour perception (for review, see Vanston &

Strother, 2016) or in working/declarative memory for colour (e.g., Morikawa & Mel, 2003; Voyer, Voyer, & Saint-Aubin, 2017) are unlikely to explain the current object memory data as both groups were matched on this variable as well as age and education. The lack of spatial memory deficits in the current aphantasic participants is consistent with previous findings that aphantasics typically self-report unimpaired spatial abilities (Dawes et al., 2020) and perform normally when these abilities are examined objectively (Bainbridge et al., 2021; Zeman et al., 2015), despite potential measurement biases toward allocentric spatial cognition. The overall lack of objective memory deficits in the aphantasic participants is unlikely to reflect data insensitivity as the standard errors for all estimates were small across the analyses.

It should be cautioned that there may have been sampling bias in the aphantasic group given that those with abnormally weak mental imagery ($VVIQ \leq 32$) were explicitly recruited. As in the present study, it is not uncommon for the majority of aphantasic participants to report a complete absence of mental imagery on the VVIQ despite allowances for individuals with weak mental imagery (Dawes et al., 2020; Zeman, Dewar, & Della Sala, 2015). Yet, when recruitment biases are explicitly controlled for, total aphantasia has been indicated to be rarer in the general population than “moderate aphantasia” (0.8% versus 3.1%, respectively; Dance, Ipser, & Simner, 2022). Thus, the strength of any potential imagery-related memory deficits are likely to have been overestimated rather than underestimated as compared to those in the true aphantasic population. Moreover, further exploratory analysis indicated the overall pattern of results was not affected by the severity of aphantasia as determined by varying the VVIQ cut-off score(s) and task-based memory vividness ratings used to define it. However, while clear and objective imagery deficits have been previously found in small samples of aphantasics (e.g., $n = 15$; Keogh & Pearson, 2018), whether memory should be impaired to a similar extent with aphantasia is unclear given the paucity of objective memory studies (see Bainbridge et al., 2021; Monzel, Vetterlein, & Reuter, 2022; Pounder et al., 2022).

The present study is not the first to find little to no objective evidence for memory impairment in people with aphantasia (but see Monzel, Vetterlein, & Reuter, 2022, who found a general impairment of verbal as well as visual short-term and long-term memory). In a recent study, Pounder et al. (2022) administered various visuospatial working memory and episodic recognition memory tasks from the Cambridge Neuropsychological Test Automated Battery (Robbins et al., 1994) to aphantasics and controls. Pounder et al. found no differences

between aphantasics and controls on any of the tasks, including verbal and visual pattern recognition memory. Although recognition memory tasks can be completed with good accuracy based on the vague sense of familiarity rather than detailed recollection (e.g., Addante, Ranganath, & Yonelinas, 2012), which is assumed to involve mental imagery in most individuals, the stimuli used in the visual pattern recognition task were complex, abstract, and thus not easily represented verbally or symbolically. Such explanations are harder still to justify for the present study due to the more challenging continuous visuospatial nature of the memory assessment, although the use of everyday objects might have enabled verbal strategies to support performance, at least in part. Like the current study, Pounder et al. (2022) also found no performance differences on any of their neuropsychological tasks when only aphantasic participants reporting a complete lack of imagery were re-analysed, although a group difference did emerge for response time in the mental rotation task, as in a case of acquired aphantasia reported by Zeman et al. (2010). Finally, while the present study concerned episodic memory, others have failed to find deficits in aphantasics in visual working memory tasks (Jacobs, Schwarzkopf, & Silvanto, 2018; Keogh, Wickens, & Pearson, 2021), which is surprising given the assumed reliance of visual working memory on visual mental imagery (Albers et al., 2013). Together, these findings suggests that, regardless of the degree of their self-reported imagery deficits, some aphantasics can perform comparably to those with typical mental imagery on tasks traditionally thought to require mental imagery.

Yet, aphantasics frequently self-report difficulties with ABM in large sample online questionnaire-based studies (Dawes et al., 2020; Milton et al., 2021; Zeman et al., 2020). Moreover, Dawes et al. (2022) recently used a modified version of the Autobiographical Interview (Addis, Wong, & Schacter, 2008) to show that aphantasics recalled specific ABMs that were less vivid and lacking in sensory and spatial detail. These aphantasics also reported their recall to be devoid of a particular visual perspective, indicating their profound imagery deficits. Dawes et al. (2022) further showed the ability to imagine future events was similarly affected in people with aphantasia (as in Dawes et al., 2020), but to a greater extent than recalling real personal events, which was taken as evidence for a general imagery-based deficit in constructing events. Interestingly, the aphantasics in Dawes et al.'s (2022) study rated real and imagined events as less coherent and lacking in emotion, possibly due to the absence of a particular visual perspective (Williams & Moulds, 2008), yet found them no less personally meaningful than did controls. Considering this line of evidence, the disagreement

between these studies and the present one (as well as Pounder et al., 2022) may be explained by the method of assessing episodic memory. As noted in the previous chapter, the episodic events generated from 3D memory tasks may be more naturalistic in some respects than those from more standard episodic memory tasks, but autobiographical memories should naturally elicit a greater sense of reliving and more vivid mental imagery than both due to the greater personal meaningfulness of such episodes. Indeed, there may be multiple forms of episodic memory, with ABM recall engaging the default mode network, which is associated with an assortment of subjectively meaningful introspective mental activities, whereas standard task-based episodic retrieval of materials encoded in the laboratory recruits frontoparietal regions (Chen et al., 2017; Roediger & McDermott, 2013). However, this explanation is difficult to reconcile with the selective task-based object memory deficits found in a large sample of aphantasics by Bainbridge et al. (2021).

One, potentially more compelling, explanation for the present findings is that some aphantasics might have a latent capacity for mental imagery, which they have no awareness of, but nevertheless supports a normal level of task performance (Nanay, 2021; Pounder et al., 2022). While the notion of unconscious mental imagery runs counter to the view that mental imagery is necessarily conscious (Farah, 1984; Kosslyn, 2005), more current thinking has entertained this possibility (Brogaard & Gatzia, 2017; but see Kind, 2021). Visual perception, which shows behavioural and neural overlap with visual mental imagery (Pearson, 2019; Pearson et al., 2015), may occur without conscious awareness (e.g., Kiefer et al., 2011), although this concept is, like that of unconscious mental imagery, controversial (Peters et al., 2017). For example, disrupted primary visual cortex function in blindsight patients (see Leopold, 2012 for review) or in neurologically healthy individuals with non-invasive brain stimulation (Boyer, Harrison, & Ro, 2005) can abolish conscious visual perception while preserving the ability to respond to visual stimuli. More direct evidence for unconscious visual mental imagery is currently scarce, possibly due to assumptions about the nature of mental imagery. However, Kwok et al. (2019) recently showed that both the active imagining and successful imagery suppression of visual stimuli results in comparable levels of binocular rivalry priming in typical imagers. Critically, Kwok et al. showed the perceptual presentation of an irrelevant neutral luminous stimulus during active imagery and imagery suppression, which should interfere only with imagery-based priming in the active imagery condition, also affected priming in the imagery suppression condition. Using a similar imagery suppression paradigm, Koenig-Robert & Pearson (2020) were further able to decode

the content of mental imagery using multivoxel pattern analysis visual brain areas despite subjects reporting successful imagery suppression, although the subjective nature of such reports and small sample size should be noted. In another study using the same analytical methods (Koenig-Robert & Pearson, 2019), both the contents and vividness of mental imagery could be decoded from activity patterns in primary visual cortex up to 11 seconds before making conscious mental imagery-based judgements. Together, these findings suggest that involuntary and non-conscious mental imagery can contribute to task performance in typical imagers.

Consistent with differences in metacognitive awareness of mental imagery, some aphantasic participants in the present experiment ($n = 4$) remarked on the surprising ease with which they completed the object and/or spatial memory components of the task, despite not being able to say how they did so. Other aphantasic participants could describe the strategies they employed, which included verbal or semantic strategies as expected, but these strategies did not differ from the kind used by control participants (e.g., verbally encoding the colour of objects or assigning object positions to numbers on a clockface). Additionally, there were no significant group differences in RT, a measure which has previously been used to detect alternative non-imagery-based strategy use in aphantasics. However, the strongest evidence for poor metacognitive awareness of mental imagery in the present aphantasics comes from the high level of precision with which they remembered visual object features (i.e., colour hue), which was comparable to that of the control participants, despite their reduced subjective vividness ratings. As noted previously, selective object imagery deficits are frequently reported by aphantasics (Bainbridge et al., 2021; Dawes et al., 2020; 2022; Keogh & Pearson, 2018), which Bainbridge et al. (2021) further showed can carry over into memory for object features. While alternative strategy use has been favoured in previous studies as an explanation for unimpaired performance on tasks thought to require mental imagery by aphantasics (Jacobs, Schwarzkopf, & Silvanto, 2018; Keogh, Wickens, & Pearson, 2021; Zeman et al., 2010), none have until now examined the fidelity of visual representations, which should be more sensitive to imagery-based memory impairments when using continuous measures such as retrieval precision. It should be acknowledged, however, that alternative mixture models to the one used here can also be applied to continuous report data (e.g., Bays, 2014), but two-component models describe this type of data well and have previously been used to behaviourally and neurally separate long-term memory retrieval success and precision in various populations, including healthy younger adults (Brady et al.,

2013; Cooper et al., 2017; 2019; Harlow & Yonelinas, 2016; Korkki et al., 2020; 2022; Richter et al., 2016; Stevenson et al., 2018; Sutterer & Awh, 2016). Moreover, the current results did not change when a model-free measure of object memory performance, raw angular colour deviation, was analysed. Thus, the present data is the first to show high-fidelity visual representations may be intact and accessible at a subconscious level in some self-identified aphantasics.

Many individuals with aphantasia report experiencing involuntary mental imagery, either as flashes during wakefulness or during dreaming (Dawes et al., 2020; Milton et al., 2021; Palermo et al., 2022; Zeman, Dewar, Della Sala, 2015; Zeman et al., 2020), further supporting the notion that some aphantasics may possess a capacity for mental imagery necessary to support normal imagery-based task performance. However, the VVIQ, a self-report measure commonly used to identify aphantasia, explicitly requires respondents to intentionally generate mental images and thus fails to distinguish between those who can and cannot form involuntary mental imagery. Additionally, tasks involving the intentional generation of imagery such as the one used by Keogh & Pearson (2018), where imagery was cued, may obscure this latent capacity in some aphantasics. At surface, this view is harder to reconcile with frequent reports made by aphantasics of ostensibly imagery-related deficits in ABM, which is often spontaneously recalled (Berntsen, 2021). These reports might reflect the way ABM is probed, which sometimes involves the intentional recall of specific events (as in the custom version of the Autobiographical Interview used by Dawes et al., 2020; 2022). However, aphantasics additionally report deficits on the SAM questionnaire, which assesses ABM ability more generally (used here and also by Dawes et al., 2020), as well as indicate less frequent involuntary memory intrusions than typical imagers (Dawes et al., 2020). However, it should be cautioned that, more generally, individuals may be less willing or confident to report conscious imagery that is weak or dim because it is near the threshold for consciousness (Deroy, 2020). While the debate over the precise nature of aphantasia is far from resolved, the condition may be best characterised by differences in imagery phenomenology, although it may be speculated that some aphantasics might still have deficits in mental imagery ability commensurate with their imagery experience. More objective measures of imagery ability such as binocular rivalry priming from visual mental imagery (Keogh & Pearson, 2018), skin conductance during imagined frightening scenarios (Wicken, Keogh, & Pearson, 2021), or pupillary light response to visual mental imagery (Kay et al.,

2022), should be included in future studies to distinguish metacognitive forms of aphantasia from other possible subtypes.

The present findings also pose a challenge to a recent proposal that aphantasia might reflect deficits in the episodic system rather than in mental imagery *per se* (Blomkvist, 2022). This theory extends the constructive episodic simulation hypothesis (CESH; Schacter & Addis, 2007; 2020), where episodic memory retrieval and imagery generation are held to involve common constructive and simulative processes (Hassabis, Kumaran, & Maguire, 2007; Hassabis & Maguire, 2007; Pearson, 2019), by adding (1) hippocampally-based memory indices that point to the storage locations of individual episodic elements, (2) multiple modality-specific episodic retrieval processes, and (3) separate episodic and semantic spatial retrieval processes. Under this expanded cognitive architecture, termed CESH+, Blomkvist distinguishes between aphantasics with voluntary mental imagery deficits and aphantasics with mental imagery deficits irrespective of volition. Specifically, Blomkvist argues that the former type of aphantasics reflects an impairment in activating the episodic system to generate mental imagery in a top-down manner only. By contrast, the latter type of aphantasics might be deficient at both top-down and bottom-up imagery generation (i.e., reflecting impaired access to the episodic system) or, alternatively, have an impaired episodic system on its own. Blomkvist notes that, in the case of more “complete” aphantasia, there is currently insufficient evidence to favour one possibility over the other. In the present study, the observation that aphantasic participants were unimpaired in both object and spatial components of memory task argues against more fundamental episodic memory deficits (see also Pounder et al., 2022).

As suggested by CESH+, compensatory reliance by aphantasics on an unimpaired semantic system to complete episodic memory tasks should also lead to less precise recall in general, yet the aphantasic participants in the current study were capable of recalling randomly varying object colour hues with comparable precision to non-aphantasic controls. Furthermore, these object stimuli were selected for their lack of specific colour associations, thereby rendering pre-existing knowledge of an object’s stereotypical colour uninformative in the object memory component of the task. While it is difficult to imagine how the aphantasics participants completed the current memory task without the use of mental imagery, it is nevertheless possible that they did so using a strategy that has yet to be identified. Ruling out the possibility of alternative strategy use is of critical importance to future research on the question of unconscious mental imagery, as a true lack of mental imagery in the current

aphantasic participants would raise questions about the importance mental imagery in episodic memory function more broadly. Efforts to this end may be hindered, however, due to the observation that many of the aphantasic participants could not articulate how they completed the memory task components, and when they could, they did not differ from controls in the strategies they employed as noted previously. However, a lack of conscious awareness of detailed sensory memory representations would reduce the sense of subjective memory reliving, which may explain the potentially greater tendency for aphantasics to self-report episodic memory deficits on questionnaires that often require respondents to recall autobiographical events, but not always exhibit deficits on more objective episodic memory tasks, which vary to a greater extent in terms of promotion and/or assessment of subjective memory reliving.

Turning to the exploratory correlation analyses, the absence of significant association in the aphantasics participants between VVIQ and vividness ratings in either component of the memory task suggests these measures may not have tapped the same constructs of mental imagery in both groups. More generally, global measures of ‘trait vividness’ such as the VVIQ do not always show a relationship with ‘state vividness’ as measured by task-based trial-by-trial ratings (for a recent meta-analysis, see Runge, Cheung, & D’Angiulli, 2017). Furthermore, D’Angiulli et al. (2013) showed the VVIQ to correlate only with static and not dynamic scene imagery vividness ratings, the latter of which was suggested to place greater demands on working memory, thereby reducing the amount of cognitive resources available for metacognitive judgements. This might explain the lack of a relationship between vividness ratings and the VVIQ in the current aphantasics, as the memory task involved some dynamic imagery due to the environmental interaction it encouraged, but it is not clear why the imagery groups would have differed in this respect. In the present study, the task-based vividness ratings are unlikely to reflect post-retrieval monitoring processes such as memory confidence as they were made before rather than after feature reproduction (Richter et al., 2016). However, while the overall level of performance was good, the aphantasic participants might still have used the vividness ratings as a proxy for retrieval effort or perceived task difficulty given these ratings generally tracked memory performance, potentially reflecting a lack of awareness of their imagery.

The stronger significant relationship observed in the control participants between VVIQ and spatial memory vividness instead of object memory vividness was unexpected given the VVIQ’s putative emphasis on visual mental imagery. While effort was made to

match the language of the VVIQ to the vividness ratings scale used in the current memory task, this might have had the unintended consequence of biasing spatial memory vividness ratings toward visual mental imagery. It is also possible that, despite instructions to rate only the vividness of a given target object's remembered study location before spatial feature reproduction, participants with typical imagery might have instead imagined the entire scene. Spatial information has previously been suggested to serve as a scaffold for episodic memory and may be particularly effective as a retrieval cue, facilitating scene reconstruction (Robin, 2018). For example, ABM recall is faster and more episodically rich when cued by specific place cues versus general thematic cues (Sheldon & Chu, 2017). Furthermore, spatial information is recalled early during episodic memory retrieval, and recollection is more detailed and vivid when it is cued by locations versus objects (Hebscher, Levine, & Gilboa, 2018) or versus people (Robin, Wynn, & Moscovitch, 2016). While this might explain the stronger correlation between VVIQ and spatial memory vividness ratings in the control participants, it is more difficult to reconcile with the lower overall vividness ratings for spatial memory features in both imagery groups.

Concerning episodic memory more generally, the greater precision of first-person versus third-person object memory retrieval in both imagery groups is intriguing. This difference was not significant when raw object memory errors or overall retrieval success were analysed separately, suggesting a first-person perspective might impact the fidelity with which memories are retrieved specifically. While the overall level of vividness for spatial memory features was lower than that for object memory features, and further exploratory correlation analysis revealed both first-person and third-person object memory recall performance to be significantly related to vividness ratings in the control participants, who presumably had intact mental imagery metacognition, this relationship was comparatively stronger for object features studied in first person. By contrast, the same relationship for spatial memory features was significant for all trial types, except for those studied and tested in a first-person perspective (i.e., stay first person trials). This pattern of correlations for the spatial memory component of the task may be due to stay first person trials reflecting egocentric spatial representations in their purest form, which may lead to worse spatial memory performance and less vivid spatial recall in comparison to allocentric representations. When considered together, these results suggest that episodic memory reliving may be promoted more by the greater quality representations of scene contents formed when experienced in first person, rather than by a first-person (egocentric)

perspective on its own. This interpretation is broadly consistent with that of Aydin (2018), who suggested object imagery to be recruited in ABM tasks requiring self-reflective processing, whereas spatial imagery might support direct retrieval of episodic details. However, further work is needed to disentangle the relative contributions of object versus spatial imagery as well as retrieval perspective to subjective episodic memory reliving.

Further research is needed to explore the possibility of unconscious mental imagery in aphantasics. In particular, the application of the imagery suppression paradigm (Kwok et al., 2019) and multivoxel pattern analysis (Koenig-Robert & Pearson, 2019) to this question promises further insights. Additionally, with different paradigms, more sophisticated measures of metacognitive efficiency (Fleming & Lau, 2014; Fleming, 2017) can be leveraged to examine the trial-wise correspondence between subjective memory vividness or confidence ratings and objective memory performance whilst accounting for overall task performance and response bias (Ye et al., 2018; Zou & Kwok, 2022). Furthermore, individuals with metacognitive aphantasia may be particularly amenable to imagery training, which has previously been indicated to improve visual mental imagery abilities in conditions such as multiple sclerosis and Alzheimer's disease as well as in old age (Ernst et al., 2013; Hussey et al., 2013; Vranic, Martincevic, & Borella, 2021; but see Rademaker & Pearson, 2012). Another promising avenue of future research relates to the multisensory imagery deficits reported by many self-identified aphantasics (Dawes et al., 2020). Whether imagery deficits in other sensory modalities significantly contribute to aphantasia-related self-reported episodic memory deficits remains unaddressed, but is worth investigating given the proposed importance of multisensory retrieval in typical episodic memory reliving (Simons, Ritchey, & Fernyhough, 2022). Yet another line of future inquiry concerns the possibility of a spatial subtype of aphantasia (Palermo et al., 2022). As noted by Palermo et al., the current use of the VVIQ to identify individuals with atypical imagery may introduce sampling bias favouring those with object imagery deficits over spatial imagery deficits. A spatial subtype of aphantasia is possible in principle given the dissociation between object and spatial imagery (Luzzatti et al., 1998). Moreover, broader scene imagery constitutes an integral part of episodic processing and typically involves both visual and spatial types of mental imagery (Barry et al., 2019). Therefore, whether episodic memory is impaired in spatial aphantasics also warrants investigation. More generally, how first-person visuospatial imagery might facilitate other aspects of episodic memory (e.g., object imagery), which in turn may lead to a stronger feeling of reliving, begs further study.

To conclude, this study is among the first to investigate episodic memory in aphantasics using objective and subjective measures. A novel 3D object and spatial memory task that manipulated visuospatial perspective was employed, but no evidence for impairment in either aspect of memory were found. This adds to recently emerging evidence for one possible subtype of aphantasia (among potentially many) in which mental imagery is intact and supports accurate task performance, but is not consciously accessible (Pounder et al., 2022). More work is needed to address the evidently heterogenous nature of the condition, although the study of individuals with both atypical imagery experience and/or ability offer the promise of gaining further insight into the factors necessary for subjective episodic memory reliving (Simons, Ritchey, & Fernyhough, 2022) as well as wider autonoetic consciousness (Zaman & Russell, 2022). Finally, further work is needed to identify the neural basis of mental imagery in general and aphantasia in particular.

Chapter 5: General Discussion

Summary of Findings

This thesis aimed to gain further insight into the factors underlying the subjective reliving of episodic memory and its parietal neural substrates. According to the subjective experience of remembering hypothesis (Simons, Ritchey, & Fernyhough, 2022), posterior parietal cortex (PPC) regions such as the angular gyrus (AnG) support the subjective reliving of episodic memory by integrating multisensory event features within an egocentric (i.e., self-referential) framework during retrieval. To this end, I developed three experiments in which I tested different populations using different methods to address the following questions: does the left AnG support a domain general mechanism of multimodal integration (Chapter 2), what are the contributions of the AnG and precuneus to first-person episodic memory retrieval (Chapter 3), and are there differences in the visuospatial perspective and vividness of episodic memory retrieval in individuals with mental imagery deficits (Chapter 4)? Here, the findings from these three experiments will first be summarised, then considered with respect to other theories of parietal mnemonic function. Finally, I will discuss outstanding research questions and future research directions motivated by findings from this work as well as those of the wider literature.

In Chapter 2, I presented my first experiment where I used non-invasive brain stimulation to test the causal role of the left AnG in multimodal feature integration during episodic and semantic memory retrieval. In this study, continuous theta burst stimulation (cTBS) was applied offline to left AnG target and vertex control sites before the retrieval phase of a newly-designed associative memory task. The effects of stimulation on episodic associative recognition and semantic relatedness judgements, made on the same unimodal and multimodal object pairs, was then examined. AnG cTBS was found to selectively modulate multimodal versus unimodal response times (RTs) in both declarative memory retrieval tasks, indicating the region may process multimodal information similarly across different forms of declarative memory retrieval. Inconsistent with the predicted inhibitory cTBS effect, however, AnG stimulation facilitated RTs. Furthermore, the observed stimulation effect on RTs in both retrieval tasks was not accompanied by differences in objective or subjective measures of episodic memory performance.

In Chapter 3, I investigated the effects of normal ageing on the first-person perspective episodic memory retrieval and its parietal neuroanatomical correlates.

Accordingly, I tested neurologically healthy younger adults (YAs) and older adults (OAs) using a custom 3D object location memory task that manipulated visual perspective during both study and test. The OAs were found to have a general deficit in first-person (egocentric) retrieval, irrespective of the original encoding perspective. A more subtle age-related deficit was apparent in third-person (allocentric) retrieval, but only when the original encoding perspective was also third person. Additionally, the OA structural scan data was analysed using voxel-based morphometry (VBM) to test several hypotheses regarding the role(s) of the precuneus and AnG of the parietal lobes in episodic memory. In the more restrictive *a priori* analyses, grey matter volume within the left AnG and the precuneus was positively correlated in OAs with the specific adoption of a first-person retrieval perspective. Furthermore, the volume of both parietal regions was shown to decline with age.

Lastly, in Chapter 4, I explored the effects of aphantasia, a non-clinical condition characterised by a deficit in voluntary visual mental imagery, on the visuospatial perspective of episodic memory. Motivated by previous reports indicating selective object (i.e., visual) imagery deficits, the 3D object location memory task used in Chapter 3 was modified to allow a more holistic assessment of memory for both object and spatial object features under different perspective conditions. Aphantasics showed no objective performance impairments relative to non-aphantasic control participants in either aspect of memory, despite rating their overall subjective memory vividness lower. This suggests some aphantasics might lack conscious awareness of mental imagery rather than have a deficit in mental imagery itself. More broadly, both aphantasic and control participants remembered visual object features more precisely when studied in first person than third person, suggesting that a first-person perspective might facilitate episodic memory reliving by enhancing the representational quality of remembered scene contents.

Implications of Findings

To the best of my knowledge, the finding reported in Chapter 2 that left AnG cTBS modulated multimodal versus unimodal response times during associative episodic and semantic memory retrieval provides the first causal brain stimulation evidence for an AnG-mediated domain-general mnemonic retrieval process, although further corroboration of this result is needed, ideally using alternative measures. Additionally, it should be cautioned that these RT effects were not associated with the level of stimulation administered to participants. More critically, it should be noted that the importance of the AnG in semantic processing has recently been questioned (Humphreys et al., 2017; 2022; Humphreys, Jung, &

Lambon Ralph 2022; Humphreys & Tibon, 2023, Lambon Ralph et al., 2017). As the same testing materials were used in both declarative memory tasks of the study reported in Chapter 2, the RT effect in the semantic relatedness task may reflect incidental episodic memory retrieval rather than semantic processing. However, it should also be noted that the RT effect was relatively stronger in the semantic relatedness task, which should capture episodic memory retrieval processes less purely than the associative recognition task. Furthermore, further analysis indicated little involvement of recollection in associative recognition task performance, an aspect of episodic memory the AnG is more widely accepted to support (for reviews, see Hutchinson et al., 2009; Vilberg & Rugg, 2008; Wagner et al., 2005). Finally, no significant differences were found in exploratory analyses testing for opposing RT effects in the different retrieval tasks, which is inconsistent with non-semantic accounts for AnG function. Thus, future investigation of domain-general accounts for AnG function should endeavour to more fully separate different processes of interest, but the present RT findings are broadly consistent with proposals that the region might function as a multimodal integrative hub supporting different cognitive domains (Seghier, 2013).

While AnG-mediated integrative multisensory processing may be an important factor underlying rich and holistic subjective re-experiencing of episodic memories (Simons, Ritchey, & Fernyhough, 2022), such a view must account for other more established integrative hubs like the bilateral anterior temporal lobes (Lambon Ralph, 2013; Lambon Ralph et al., 2017; Lambon Ralph & Patterson, 2008; Patterson & Lambon Ralph, 2016; Patterson, Nestor, & Rogers, 2007; Rogers et al., 2006; Visser, Jeffries, & Lambon Ralph, 2010). Indeed, disrupted anterior temporal lobe function appears to affect semantic processing more globally than disrupted AnG function. For example, circumscribed anterior temporal lobe atrophy in semantic dementia patients has been shown to impair semantics across various input and output modalities (Bozeat et al., 2002; 2003; Coccia et al., 2004; Jefferies & Lambon Ralph, 2006; Lambon Ralph et al., 2001; Rogers et al., 2006). Repetitive TMS of the anterior temporal lobes has likewise been demonstrated to disrupt the semantic association judgements for words and pictures, irrespective of the targeted hemisphere (Pobric, Jefferies, & Lambon Ralph, 2010).

Given the AnG's connectivity with modality-specific sensory association cortices, the region has been proposed to function as a heteromodal hub where different sensory-motor inputs converge (Bonner et al., 2013; Seghier, 2013). The finding from Chapter 2 that the processing of multisensory audio-visual stimuli during different forms of declarative memory

retrieval was modulated by AnG cTBS, along with previous evidence indicating an apparent preference for multisensory information during episodic memory retrieval (Bonnici et al., 2016; Yazar, Bergström, & Simons, 2017), supports this view. Therefore, the AnG may be particularly sensitive to sensory information, serving as a lower-order heteromodal hub where these features may be abstracted into higher-order amodal conceptual representations supported by the bilateral anterior temporal lobes in the case of semantic memory (Fernandino et al., 2016). This would align with multi-hub theories of semantic memory such as the dynamic multilevel reactivation framework (Reilly et al., 2016; but see also Damasio, 1989; Tranel, Damasio, & Damasio, 1997), which emphasises the importance of interactions between lower-order sensorimotor representations supported by the AnG (also the posterior middle temporal gyrus) and higher-order amodal representations within the anterior temporal lobes. The degree of interactivity between these hubs and the modality-specific spokes to which they are linked may vary depending on task demands.

The finding from Chapter 2 that AnG cTBS modulated response times in different declarative memory retrieval tasks involving time-extended audio/visual stimuli, presented sequentially over the span of several seconds, may also be compatible with unifying online information buffering accounts, namely the parietal unified connectivity-biased computation (PUCC) model (Humphreys & Lambon Ralph, 2015) and its more recent instantiations (Humphreys, Lambon Ralph, & Simons, 2021; Humphreys & Tibon, 2022). However, it should be noted that information buffering and integration accounts may not necessarily be mutually exclusive, as the former type of processing may support the latter. According to the PUCC model, the AnG supports the dynamic online multimodal buffering of spatiotemporally extended information. Consistent with information buffering accounts, fMRI activity in the ventrolateral parietal cortex increases with the duration of stimulus presentation (Vilberg & Rugg, 2009a) and is sustained while information is maintained during recollection (Vilberg & Rugg, 2012; 2014), motivating episodic buffer-type proposals (for review, see Rugg & King, 2018). More recently, activity in the left AnG has also been associated with time-extended semantic integration during narrative reading (Branzi et al., 2020), which is disrupted with online TMS applied to the same region (Branzi et al., 2021), suggesting a more general role in information buffering as proposed by the PUCC model. The PUCC model and its extensions may also provide alternative explanations for previous findings interpreted as evidence favouring integrative accounts. For example, whereas Bonnici et al. (2016) found the AnG to be preferentially activated during the more definite

time-extended mental replay of multimodal audio-visual clips, no such preference was found during the generation of multimodal semantic word associations. More broadly, the PUCC model may help reconcile content (e.g., Rugg & King, 2018) and attentional (e.g., Cabeza, Ciaramelli, & Moscovitch, 2012) accounts for ventrolateral parietal cortex function, as bottom-up capture of attention may result from the automatic buffering of incoming information (Humphreys & Lambon Ralph, 2017). However, more explicit temporal manipulations are needed in future casual brain stimulation experiments.

It should be acknowledged that findings made since the conception of the study presented in Chapter 2 raise questions as to whether the AnG functions as a semantic hub. Using a within-subjects design fMRI study, Humphreys, Jung, & Lambon Ralph (2022) compared several AnG activation across several domains relative to rest, which served as common baseline. They found that while the AnG is strongly engaged when making episodic retrieval judgements concerning studied object features, the region is disengaged when making semantic decisions on which of two alternative features most accurately describe some property of an object, suggesting the region may not be critically involved in semantic processing. However, the appropriateness of rest as a baseline condition has been criticised by others (Stark & Squire, 2001; Morcom & Fletcher, 2007) as it too may involve some degree of semantic processing, which may account for the inconsistency sometimes observed in AnG response polarity (Kuhnke et al., 2023). Furthermore, the level of AnG deactivation has, unlike episodic memory tasks (King & Rugg, 2018), been noted to correlate with difficulty in semantic and perceptual/spatial tasks (Humphreys & Lambon Ralph, 2017; Kuhnke et al., 2023), but this may not hold universally across the AnG (Kuhnke et al., 2023). In the context of episodic memory encoding, however, multivoxel pattern analysis has suggested that reductions in univariate ventral parietal cortex activity within the vicinity of the AnG may still accompany content representations (Lee, Chun & Kuhl, 2017). Thus, the significance of semantic task-based deactivations in the AnG is presently unclear, although the above evidence suggests the importance of accounting for task difficulty, which may alternatively explain interpretations of many classic semantic contrasts (e.g., word versus pseudoword or abstract versus concrete word judgements) (Humphreys & Tibon, 2022). Moreover, it is possible that AnG-mediated information buffering may not be necessary for less challenging semantic tasks, which may instead recruit other parts of the semantic network.

Affirming the importance of the AnG to episodic retrieval, Humphreys, Jung, & Lambon Ralph (2022) additionally correlated activity within the region with item-specific memory vividness ratings. In another fMRI study, Humphreys et al. (2022) similarly made cross-domain comparisons, but using a propositional speech production paradigm to investigate AnG function based on its output (i.e., generating descriptions based on prompts tapping into different domains) rather than its inputs (e.g., object images or spoken words). They found that the AnG was recruited only when propositional speech production involved drawing from autobiographical memory and not object or event semantics, corroborating the results of a concurrent probabilistic functional neuroimaging meta-analysis. Critically, AnG activation in their task was also found to increase with the demands placed on autobiographical memory recall, which stood in contrast to the ATL, a more established semantic hub, where activity did not vary across the experimental conditions, likely reflecting the common involvement of semantics. However, further cross-domain comparisons such as these are needed.

Anatomical, connectivity, and functional parcellations of the AnG suggest the existence of multiple distinct subregions (Caspers et al., 2006; 2008; Humphreys, Jackson, & Lambon Ralph, 2020; Nelson et al., 2010; 2013; Seghier, 2013; Uddin et al., 2010), the functional implications of which have only relatively recently started being investigated. For instance, mnemonic accumulator or familiarity-type functions previously ascribed to the intraparietal sulcus have also been suggested to extend into the dorsal AnG (Crowe et al., 2013), whereas the ventral AnG remains strongly associated with recollection (Sestieri et al., 2017). Anterior/posterior subdivisions have also been identified. For example, Bonnici et al. (2016) showed that whereas multimodal episodic memory retrieval recruited an anterior AnG subregion, more posterior and ventral subregions were associated with semantic retrieval. Thus, the apparent domain-general nature of AnG processing indicated by the cTBS study presented in Chapter 2 might simply reflect limitations in the anatomical specificity of transcranial magnetic stimulation (TMS) at the subregion level, as target sites should ideally be separated by 10mm or more (Sliwinska, Vitello, & Devlin, 2014).

According to a recent review by Humphreys & Tibon (2022), the wider lateral parietal cortex including the AnG may support a core process or mechanism (i.e., online multimodal information buffering), the expression of which may vary, however, depending on regional/subregional differences in structural connectivity with other cognitive networks, emphasising the need to synthesise regional and network-based approaches. Such

connectivity differences may explain why the AnG seemingly preferentially processes different kinds of information such as multisensory features (Bonnici et al., 2016; Yazar, Bergström, & Simons, 2017) or egocentric information (Bonnici et al., 2018; Ciaramelli et al., 2010b; Russell et al., 2019), despite supporting an ostensibly domain-general underlying process (Humphreys, Lambon Ralph, & Simons, 2021). Of relevance to the subjective experience of remembering hypothesis, recent diffusion tensor imaging as well as resting-state and task-based connectivity analyses (Humphreys, Jackson, Lambon Ralph, 2020; Humphreys, Jung, & Lambon Ralph, 2022) suggest further functional subdivisions within the ventral portion of the AnG, identifying a mid-subregion showcasing connectivity with key nodes in the default mode and core recollection networks, including the precuneus.

The precuneus is anatomically linked to the AnG via the occipitofrontal fasciculus (Makris et al., 2007) and, in addition to belonging to the default mode network (Buckner, Andrews-Hanna, & Schacter, 2008) and core recollection network (Hayama, Vilberg, & Rugg, 2012; Johnson & Rugg, 2007), both PPC regions are members of a wider posterior medial network that is thought to support the construction of mental scenes from an egocentric viewpoint (for reviews, see Ritchey & Cooper, 2020; Ritchey, Libby, & Ranganath, 2015; Ranganath & Ritchey, 2012). Furthermore, functional neuroimaging findings frequently implicate the precuneus in first-person perspective visual mental imagery across a range of tasks as well as successful episodic memory retrieval (see Cavanna & Trimble, 2006 for review). Therefore, interactions between the precuneus and AnG may support first-person perspective episodic memory retrieval, an important aspect of subjective memory reliving (Simons, Ritchey, & Fernyhough, 2022; Zaman & Russell, 2022). In light of the above evidence, it is proposed that the precuneus may facilitate rich recollective experiences by providing vivid first-person perspective mental imagery to the AnG for integration and/or buffering within a broader egocentric framework during remembering. By contrast, spatial transformations from hippocampally-supported map-like or viewpoint independent allocentric spatial reference frames to an egocentric frame of reference may be performed with the aid of posterior cingulate and retrosplenial cortices (Burgess, 2008; Epstein, 2008; Guterstam et al., 2015; Vann, Aggleton, & Maguire, 2009).

In a FreeSurfer analysis by Hebscher, Levine, & Gilboa (2018), precuneus volume, summed across both hemispheres, was found to positively correlate with the tendency to recall autobiographical memories from a first-person perspective. However, Bonnici et al. (2018) demonstrated left AnG cTBS to reduce this same tendency in healthy younger adults.

First, it was unclear from such evidence whether these PPC regions support the specific adoption of a first-person perspective or have more direct involvement in egocentric mnemonic representations. Second, the involvement of both regions in first-person perspective autobiographical memory recall made drawing functional distinctions between these PPC regions challenging. Interpretation of non-invasive brain stimulation evidence in this regard may also be complicated by the prospect of remote stimulation effects due to the connectivity between these PPC regions. Indeed, remote stimulation effects have previously been leveraged to intentionally target other regions such as the hippocampus via AnG TMS and modulate its activity as well as episodic memory encoding and retrieval (Hermiller et al., 2019; 2020; Wang & Voss, 2015). Complementary functional connectivity work is therefore likely needed to characterise the flow of information between the AnG and precuneus during egocentric memory retrieval.

St. Jacques, Szpunar, & Schacter (2017) observed fMRI activity in both the AnG and precuneus to decrease with repeated attempts at shifting from an initially dominant own-eyes perspective to an alternative observer perspective during autobiographical memory recall, suggesting involvement in egocentric perspective adoption. In another study, Russell et al. (2019) showed that patients with exclusively right-hemisphere parietal lesions are selectively impaired at discriminating between their own encoding perspective and that of an observer when viewing previously encountered 3D scenes. Additionally, Russell et al. used multivoxel pattern analysis in a separate group of healthy older adults to identify an area encompassing the bilateral AnG that was sensitive to such judgements, although it should be cautioned that a more restricted area was revealed in a healthy younger adult comparison group, suggesting the normal ageing process may affect the neural substrates underlying self-perspective judgements. However, other fMRI studies have additionally implicated the AnG, and particularly the precuneus, in shifting from an own-eyes to an observer perspective (Eich et al., 2009; Grol, Vingerhoets, & de Raedt, 2017), raising the possibility of a PPC-mediated general perspective switching mechanism that may be agnostic to the particular retrieval perspective, thus necessitating a bi-directional test of perspective switching (see the autobiographical memory evidence from St. Jacques et al., 2018, although a direct experimental manipulation of retrieval perspective as in Chapter 3 was needed).

While the VBM analysis of OA structural MRI data presented in Chapter 3 was unable to separate the contributions of the AnG and precuneus to first-person episodic remembering, possibly due to the 3D object location memory task placing little demand on

visual mental imagery, left-hemisphere grey matter volumes in both regions were found to positively correlate with performance in trials in a 3D object location memory task requiring switching from a third-person encoding perspective to a first-person retrieval perspective. No such association was revealed in contralateral PPC regions, nor were any associations found between these regions and performance in trials requiring perspective switching in the opposite direction (i.e., from third person to first person) or in trials where encoding and retrieval perspectives remained unchanged (i.e., encoded and retrieved in third person or first person). It should be cautioned, however, that no significant correlations were found when the search volumes were expanded to the whole anatomical AnG, precuneus, and a HPC control region or the whole brain, although this may be related to power issues, low sensitivity due to the number of covariates included in analyses, near ceiling effects in some of the task conditions, or long scan-test interval.

Considered together, the pattern of results from the current VBM analysis furthers understanding of the PPC's role in subjective memory reliving, suggesting involvement in the specific adoption of a first-person retrieval perspective rather than more general perspective switching (i.e., in either direction) or more direct representation of first-person memories (i.e., where a first-person perspective remained unchanged). As noted previously, however, further comparison with healthy YAs may be needed to address the possibility of age differences in these parietal neural correlates. Indeed, additional VBM analysis comparing these PPC grey matter volumes against those in healthy YAs indicated age-related decline. This was accompanied by behavioural differences where the same older adults exhibited a more general deficit in trials involving first-person retrieval, irrespective of the original encoding perspective, possibly reflecting age-related difficulties in binding spatial information across multiple vantage points (Montefinese et al., 2015) or more general age-related deficits in embodied cognition (Costello & Bloesch, 2017; Kuehn et al., 2018; Vallet, 2015).

One issue with the research presented in Chapter 3 relates to the separation of visual and spatial aspects of first-person episodic memory. While a first-person visual perspective may encourage the adoption of an egocentric spatial framework (Torok et al., 2014), these frameworks (and visual perspectives) can be flexibly switched as needed and may also exist in parallel (Burgess, 2006; Ekstrom, Arnold, & Laira, 2014; Rice & Rubin, 2011). This concern was addressed in the online behavioural study presented in Chapter 4, which explored the influence of weak mental imagery (i.e., aphantasia) on visual and spatial

components of episodic memory under different perspective conditions. The aphantasic participants reported substantially diminished general mental imagery and made globally lower vividness ratings in the memory task than non-aphantasic control participants but showed no objective deficits in visual or spatial memory performance, suggesting that some cases of aphantasia may be attributable to a deficit in meta-cognitive awareness of mental imagery rather than in mental imagery itself (as suggested in the review by Nanay, 2021). Additionally, mixture modelling, which permits separate measures of the overall probability of retrieval success and varying retrieval precision to be derived from continuous feature report tasks, revealed visual object features (i.e., colour hue) were remembered with greater fidelity in both groups when studied and tested in first person. However, it is unclear from this data whether this effect is attributable to encoding and/or retrieval processes, for which a perspective switching manipulation is needed in the object memory component task.

Although suggested by earlier subjective reports from autobiographical memory studies (e.g., Sutin & Robins, 2010), the mixture modelling evidence from Chapter 4 is the first to indicate that a first-person perspective may objectively benefit the representational quality of certain visual episodic memory features, which may in turn aid subjective memory reliving (Simons, Ritchey, & Fernyhough, 2022; Zaman & Russell, 2022). Previous fMRI findings by Richter et al. (2016), who similarly used mixture modelling but in a 2D memory task, suggest the AnG as a likely candidate for supporting detailed episodic memory representations. In their study, Richter et al. found that AnG activity tracked the precision of episodic object feature retrieval whereas activity in the HPC and precuneus tracked the success and subjective vividness of retrieval, respectively. To the best of my knowledge, however, the role of visual perspective in memory fidelity has yet to be examined from a neural perspective.

Finally, the novel finding from Chapter 4 that self-identified aphantasic and non-aphantasic control participants had comparable levels of visual object feature retrieval precision for visual object features is among the very first objective task-based evidence to indicate a metacognitive form of aphantasia, although Pounder et al. (2022) recently also published data to this effect while the present study was being conducted. In their study, Pounder et al. found that aphantasics were evidently unimpaired on a battery of ostensibly imagery-based standard neuropsychological tasks including a complex visual pattern recognition task. However, the present findings from mixture modelling provide particularly strong evidence against the alternative explanation of non-imagery-based compensatory

strategy usage and for the existence of intact (but unconscious) visual mental representations, as presumably precise visual object feature reproduction from memory requires the latter. This interpretation is supplemented by prior reports made by some aphantasics of intact involuntary mental imagery during altered states of consciousness (Dawes et al., 2020; Milton et al., 2021; Palermo et al., 2022; Zeman, Dewar, Della Sala, 2015; Zeman et al., 2020). More generally, the present findings raise questions about the assumed nature of mental imagery and its importance in episodic memory. Indeed, the present results and those of Pounder et al. (2022) seemingly contradict a recent proposal that the condition might reflect a deficit in episodic retrieval processes rather than in mental imagery *per se* (Blomkvist, 2022). However, the results of this online behavioural study need replication, ideally in the laboratory where greater control can be exercised over testing conditions. Furthermore, these findings highlight the need for more objective methods of identifying aphantasia (Kay et al., 2022; Keogh & Pearson, 2018; Wicken, Keogh, & Pearson, 2021), as well as alternative tests for the presence of involuntary and unconscious mental imagery in such individuals (Koenig-Robert & Pearson, 2019; 2020; Kwok et al., 2019), is needed. Moreover, it is currently unclear to what extent inconsistencies in findings across the aphantasia literature reflect true heterogeneity in the condition or simply methodological and/or definitional differences.

Future Directions

Future work investigating the subjective experience of memory should seek to employ more naturalistic tasks. For example, unlike the classic approach of conducting structured autobiographical interviews (Kopelman, Wilson, & Baddeley, 1989; Levine et al., 2002), head-mounted cameras permit standard memory tasks (e.g., recognition or source memory) to be applied to real-life events (see Allé et al., 2017 for review), which are likely to be more personally relevant, meaningful, and evocative by comparison to more conventional experimental scenarios. Related to this, Kapsetaki et al. (2022) found a relationship between autobiographical memory in younger adults and the ability to recognise one's own encoding perspective recorded from a wearable camera when scenes (i.e., object arrays) were experienced in-person, but not as 2D photographs. Furthermore, Marcotti & St. Jacques (2022) recently showed that reviewing photographs taken from first-person or third-person perspectives during mini-events experienced in the laboratory can alter the reported perspective of retrieval itself as well as spatial location accuracy. The pairing of inherently more multimodal real-life events with standard task-based assessments of memory may be

leveraged, for example, to extend previous work on multimodal episodic retrieval and subjective memory reliving (Bonnici et al., 2016; Yazar, Bergström, & Simons, 2017).

The usage of everyday events in memory tasks may also increase the involvement of mental imagery during episodic memory retrieval, thereby helping separate the contribution of the AnG and precuneus to first-person remembering, which may have been hampered in the study presented in Chapter 3 due to the low trial-by-trial variability in broader scene imagery (i.e., to-be-remembered scenes varied only in terms of target and landmark object identity and location). However, alternative technologies such as virtual reality may offer stricter experimental control than wearable camera-based assessments, while still permitting great flexibility in the construction of more ecologically valid testing scenarios than standard computerised memory tasks (Smith, 2019). This may be particularly useful for manipulating other factors that may facilitate subjective memory reliving such as a first-person body view and its relation to bodily self-consciousness (Bréchet et al., 2019; Gauthier et al., 2020; Iriye & Ehrsson, 2022) or simulating experiences from atypical visual perspectives (Iriye & St. Jacques, 2021), which may be difficult to achieve otherwise.

Regardless of the task employed or population studied, future work should attempt to incorporate a wider range of subjective memory measures as found in the autobiographical memory literature (e.g., Dawes et al., 2022), to better capture the multifaceted nature of subjective recollective experience and examine more specific relationships between subjective and objective aspects of episodic memory. For example, while the study presented in Chapter 2 examined AnG stimulation effects on memory confidence only, more recent work has indicated memory vividness to mediate the relationship between objective memory accuracy and confidence, and that the AnG may be important in gauging vividness but not confidence (Zou & Kwok, 2022). With regard to visuospatial perspective in episodic memory, future work should combine multiple subjective memory measures such as vividness, confidence, or recall fluency with memory tasks such as the one employed in Chapter 3 to directly test the role of perspective in different aspects of subjective memory experience. However, future work investigating visuospatial perspective in episodic memory should also be careful to account for potential task difficulty differences across different perspective conditions (as found in Chapter 3), as well as attempt to equate those conditions more closely in terms of daily experience. Finally, future work should be undertaken to test the subjective experience of remembering hypothesis (Simons, Ritchey, & Fernyhough, 2022) more holistically by assessing first-person multimodal experiences via multiple

subjective memory measures. This may be achieved by modifying the 3D object and spatial memory task presented in Chapter 4 to additionally incorporate auditory stimuli.

As suggested by Palermo et al. (2022), there may be dissociable visual and spatial subtypes of aphantasia. The scarcity of current evidence for the latter subtype of aphantasia might simply reflect a bias toward visual mental imagery during study recruitment or the tools used to identify such conditions, which have hitherto relied primarily on the Vividness of Visual Imagery Questionnaire (Marks, 1973). Indeed, Palermo et al. (2022) used the Object-Spatial Imagery Questionnaire (Blajenkova, Kozhevnikov, & Motes, 2006), which separately assesses visual and spatial imagery preferences and experiences, to identify a similar proportion of spatial and object (i.e., visual) aphantasics, with each group respectively accounting for approximately 3% of their sample. Related to this, dissociable forms of object and place imagery neglect have also been demonstrated in two patients (Palermo et al., 2009), suggesting independent systems. The potential existence of distinct object and spatial subtypes of aphantasia provides an opportunity to separate the contribution of visual and spatial aspects of mental imagery to subjective memory reliving, which may in some cases be intertwined (Torok et al., 2014; see also Chapter 3). However, alternative approaches such as explicitly varying spatial strategy use while holding visual perspective constant in individuals with typical imagery may provide an alternative approach to this issue. Finally, the roles of parietal regions such as the AnG and precuneus in these aspects of episodic memory-related mental imagery (Cavanna & Trimble, 2006; Fletcher et al., 1995; Fulford et al., 2018; Gardini et al., 2006) and their possible dysfunction in aphantasia needs further attention, as current research has hitherto concentrated primarily on the visual cortices (Pearson, 2019).

Investigation of memory at the opposite extreme of the mental imagery spectrum may also provide an alternative and complementary perspective on the subjective reliving of memory. Individuals with hyperphantasia, a condition characterised by extremely vivid mental imagery, do not always report superior retrospective and prospective memory abilities (Palermo et al., 2022), despite recalling more episodic details than both aphantasics and typical imagers as assessed by autobiographical memory interviews (Milton et al., 2021). The apparent discordance between subjective and objective memory reports in these individuals suggests that vivid mental imagery alone may not be sufficient for subjective memory reliving. However, it is difficult to rule out the influence of different developmental trajectories in imagery ability/experience on the subjective appraisal of memory. As shown by recent data collected by Dawes et al. (2022), aphantasics experience autobiographical

recall and imagine future events as less coherent and emotional than controls, but may find them just as subjectively meaningful, suggesting individuals with atypical imagery may base their subjective mnemonic judgements on different factors. Nevertheless, an experimentally controlled task-based study of episodic memory and its subjective experience has yet to be conducted on hyperphantasic individuals. The need to move beyond subjective self-report scales in this regard is highlighted by the task-based findings from Chapter 4, which provide strong evidence for metacognitive rather than imagery-based differences in some self-identified aphantasic individuals.

The related condition of synaesthesia, where the perception of a stimulus in one modality elicits mental imagery in another (for reviews, see Banissy, Jonas, & Cohen Kadosh, 2014; Ward, 2013), presents an opportunity to further explore the possible role of multimodal integration in subjective memory reliving. Indeed, synesthesia has been argued to represent a form of multimodal mental imagery (Nanay, 2020). According to hyperbinding models of synaesthesia (e.g., Hubbard & Ramachandran, 2005; Weiss, Zilles, & Fink, 2005), the parietal lobe is thought to support the anomalous cross-modal hyperbinding of veridical and synaesthetic perceptions. Consistent with this view, functional neuroimaging reviews have associated synaesthetic experience with a network of brain regions including the AnG (Rouw, Scholte, & Colizoli, 2011; for general critique, see also Hupé & Dojat, 2015). Furthermore, Jäncke & Langer (2011) conducted a graph-theoretic analysis of electrophysiological resting-state functional connectivity data and showed that the parietal lobes are more strongly interconnected in audio-visual synaesthetes than in non-synaesthetic control participants. Brain stimulation evidence has similarly implicated PPC regions in integrative synaesthetic behaviours. For example, Esterman et al. (2006) found that applying inhibitory repetitive TMS to the right parieto-occipital region, but not the contralateral site or area V1, reduced synaesthetic interference on a Stroop-based colour verification task. Muggleton et al. (2007) showed that excitatory repetitive TMS of the same region disrupted performance on a synaesthetic priming task. Finally, Esterman, Verstynen, & Robertson (2007) showed that inhibitory repetitive TMS of the right, but not the left, intraparietal sulcus decreases colour-form binding errors referred to as “illusory conjunctions” while sparing the perception of either feature. To the best of my knowledge, no study of synaesthesia has examined the effects of AnG brain stimulation on multimodal episodic memory retrieval and subjective memory reliving.

While this thesis was primarily concerned with episodic memory retrieval, whether and how the PPC may promote subjectively richer and more vivid memory reliving due to processes occurring during encoding and/or consolidation may also be worth future investigation. An early functional neuroimaging meta-review by Uncapher & Wagner (2009) suggested that ventral parietal cortex activity is, on the balance, associated with negative subsequent memory effects, although this may be reversed with shorter retention intervals. However, several later fMRI studies have reported increased activity in the AnG while participants make relational semantic encoding judgements on word pairs that is predictive of subsequent associative recollection (de Chastelaine et al., 2011; 2016; Wong, de Chastelaine, & Rugg, 2013), suggesting a possible preference for encoding relational/associative information (see Lee, Chun, & Kuhl, 2017). Furthermore, Lee, Chun, & Kuhl (2017) used multivoxel pattern analysis to show that encoding-related activity patterns within the ventral parietal cortex predicted subsequent memory performance, despite negative univariate subsequent memory effects, possibly reflecting a neural sharpening-like effect benefitting mnemonic representations. Tibon et al. (2019) recently showed that AnG activity during encoding was associated with vividly subsequent retrieval of multimodal more than unimodal pair associates. Furthermore, Tibon et al. observed AnG activity to increase in magnitude for repeated versus non-repeated associates during the study phase of their study, which was interpreted as possibly reflecting involvement in rapid memory consolidation, somewhat consistent with the cortical binding of relation activity model (Shimamura, 2011). Supporting this, van der Linden et al. (2017) showed increased functional connectivity between the AnG and lateral occipital complex during encoding as well as retrieval can enhance overnight schematic memory retention at the cost of memory specificity.

Causal non-invasive brain stimulation techniques may provide insight into whether parietally-mediated processes are necessary for successful memory encoding. Although such studies are scarce, Koen, Thakral, & Rugg (2018) demonstrated that online repetitive TMS delivered to the left AnG during the encoding of word pairs does not impair subsequent memory. However, AnG stimulation did affect confidence in incorrect associative memory judgements, suggesting processes carried out by the region during encoding may facilitate subjective aspects of later memory retrieval. In a more recent online repetitive TMS study, Branzi et al. (2021) showed that left AnG stimulation, applied between the presentation of context and target paragraphs during a narrative reading encoding task, disrupted subsequent response times, but not accuracy, in a three-alternative forced-choice memory task. The

failure to modulate memory accuracy in both studies may reflect a non-critical role for the AnG in episodic memory encoding. Alternatively, however, the effect on response times in the Branzi et al. study may indicate a sensitivity to time-extended information in line with online information buffering accounts such as the PUCC model. Thus, further research is needed to characterise the nature of information processing performed by VPC regions that might promote subsequent memory retrieval, whether these processes share similarities with those said to operate during retrieval itself, and whether these processes support memory encoding, consolidation, or both. As the aforementioned brain stimulation studies have shown, trial-locked online repetitive TMS provides the temporal specificity needed to target encoding and consolidation stages of memory, which can be combined with multimodal memory tasks such as the associative recognition task presented in Chapter 2, assuming adequate time is allowed for stimulation effects to washout before memory retrieval.

Conclusion

This thesis investigated factors underlying the subjective reliving of episodic memory and their parietal neural substrates. First, tentative evidence from the cTBS study presented in Chapter 2 implicated the AnG in domain-general processing during episodic and semantic memory retrieval. This finding may be consistent with unifying accounts of AnG function, which propose the region to serve as a multimodal integration hub or temporary online buffer of information, and warrants further research. The VBM analysis of healthy older adult structural MRI data reported in Chapter 3 suggested associations between the AnG and, to a lesser extent, the precuneus with the specific adoption of a first-person retrieval perspective. These PPC regions were also found to atrophy with age along with the more general ability to adopt a first-person retrieval perspective, regardless of the original encoding perspective. In Chapter 4, mixture modelling of data from a task that separately examined visual and spatial aspects of episodic memory retrieval under different visual perspectives suggested that a first-person perspective may increase the fidelity with which visual features are remembered. The effects of weak mental imagery on task performance were additionally explored in this study, although no objective memory differences were found, advancing understanding of aphantasia by providing among the first evidence that the condition might result from a meta-cognitive rather than a mental imagery deficit in some individuals, which may nevertheless affect subjective memory reliving. Together, these findings refine understanding of the PPC's role in memory and provide further support for the subjective experience of remembering hypothesis, where the AnG is proposed to integrate multimodal episodic memory features

within an egocentric framework. Finally, several new directions for the study of episodic memory and its subjective reliving are suggested, with an emphasis on mental imagery and its extremes.

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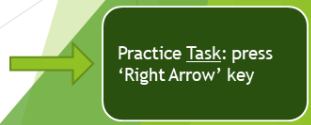
Appendix

Task Instructions for the Study Presented in Chapter 3

Note that these instructions are for the younger adult version of the task. The instructions for the older adult version were identical to the younger adult one, except for the omission of a response deadline in the test phase. The presentation of task instructions was divided into chunks so that only the relevant information was given at the start of each phase of the practice block.

Task Overview

- This task will test your memory for the positions of objects viewed from different perspectives
- Testing will be divided into 10 blocks, with each block consisting of four phases in the following order:
 - 1.) Exploration Phase
 - 2.) Study Phase
 - 3.) Arithmetic Phase
 - 4.) Test Phase
- More detailed instructions for each phase will follow in the upcoming practice block
- Instruction navigation options and keys are shown on the bottom right corner of each screen



Practice Task: press
'Right Arrow' key

Practice Block

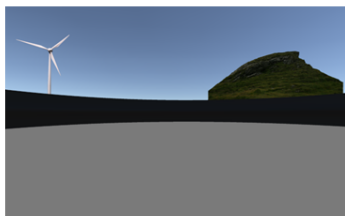
Exploration Phase Instructions

Next screen: press
'Right Arrow' key

Previous screen: press
'Left Arrow' key

Exploration Phase Overview

- You will start each block by freely exploring the testing arena, which consists of a walled circular area surrounded by four external landmarks
- You will have 15 seconds to view the testing arena from either a **first-** or **third-person perspective**, then another 15 seconds to view the arena from the alternative perspective:



First person

→
or
←



Third person

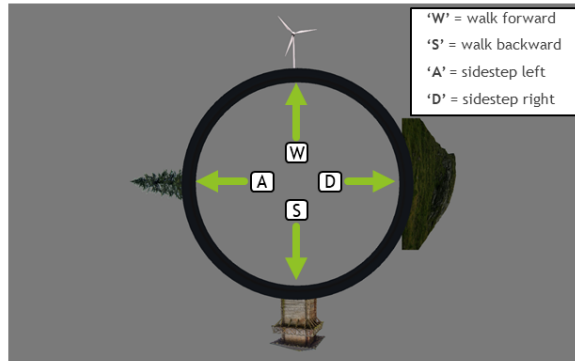
- It is important that you familiarise yourself with the testing arena during this phase as the **four external landmarks change after every block**.

Next screen: press
'Right Arrow' key

Previous screen: press
'Left Arrow' key

Movement Controls

- Use the 'W', 'A', 'S', 'D' keys to move within the arena in both perspectives:



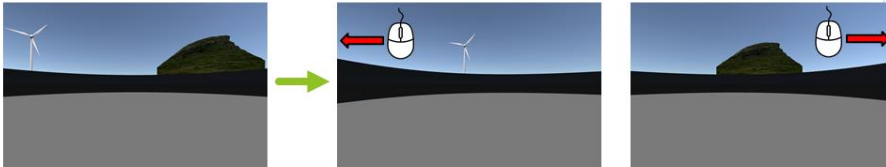
- When you hold these keys, you will initially move slowly but then get faster. You can use this to position yourself more precisely

Next screen: press
'Right Arrow' key

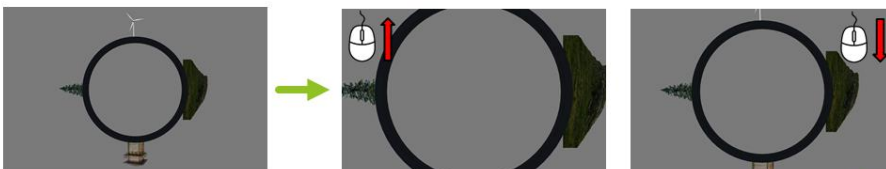
Previous screen: press
'Left Arrow' key

Camera Controls

- In first person, look left or right by moving the mouse left or right:



- In third person, zoom in and out by moving your mouse forward and backward:



Next screen: press
'Right Arrow' key

Previous screen: press
'Left Arrow' key

Summary

- Move using the 'W', 'A', 'S', 'D' keys
- Depending on your perspective, you can use your mouse to look from side-to-side or zoom in and out on the arena
- It is important that you are comfortable with these controls as they will be used throughout the memory task and help you memorise—and later recall—the object positions with greater precision
- **Press 'Space' once you are ready to practice the Exploration Phase**

Practice Exploration:
press 'Space' key

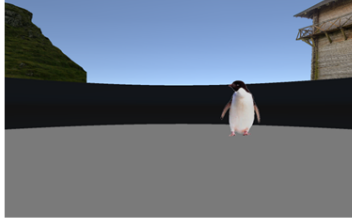
Previous screen: press
'Left Arrow' key

Practice Block Study Phase Instructions

Next screen: press
'Right Arrow' key

Study Phase Overview

- After exploring the arena, you will study objects within the arena from either first- or third-person perspectives:



or



- These objects will be shown one at a time and could be animals, tools, vehicles, food, or other common items
- You will have 10 seconds to memorise the position of each object within the arena, relative to the four external landmarks
- Use the movement and camera controls you learned in the Exploration Phase to get a better sense of each object's placement within the arena
- Press 'Space' once you are ready to practice the Study Phase

Practice Study: press
'Space' key

Previous screen: press
'Left Arrow' key

Practice Block Arithmetic Phase Instructions

Next screen: press
'Right Arrow' key

Arithmetic Phase Overview

- After studying the object positions, you will have **30 seconds** to complete simple addition and subtraction problems:

$$56 - 97 = \#\#$$

or

$$33 + 72 = \###$$

- Type your answer using the number keys and press 'Space' to respond at your own pace
- You can also press 'Backspace' to delete mistakes before submitting your answer
- Press 'Space' once you are ready to practice the Arithmetic Phase

Practice Arithmetic:
press 'Space' key

Previous screen: press
'Left Arrow' key

Practice Block Test Phase Instructions

Next screen: press
'Right Arrow' key

Test Phase Overview Pt. I

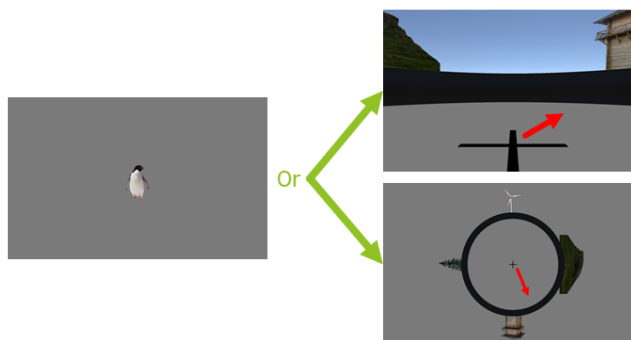
- ▶ After completing arithmetic problems, **your memory for the object positions you memorised earlier in the block will be tested from either the same or alternative perspective from which you studied them**
- ▶ There will be no new objects and the order in which they are shown will be random and different from when you studied them
- ▶ Whether an object is tested from the same or alternative study perspective will also be random

Next screen: press
'Right Arrow' key

Previous screen: press
'Left Arrow' key

Test Phase Overview Pt. II

- You will first see each object on its own for 1 second and then have *up to 15 seconds* to indicate its studied position:



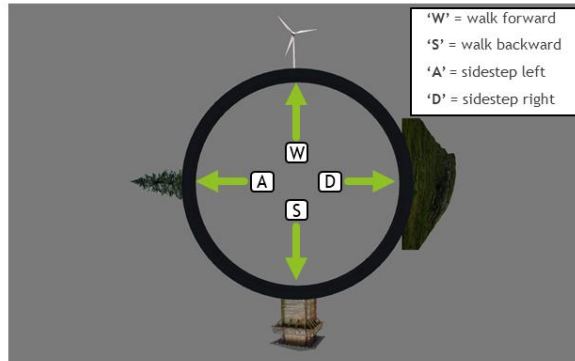
- Use the controls you learned earlier (shown in next screens) to **move the black cross as precisely as you can to where you remember studying the object** and press 'Space' to submit your response within the time limit

Controls reminder:
press 'Right Arrow'
key

Previous screen: press
'Left Arrow' key

Movement Controls Reminder

- Use the 'W', 'A', 'S', 'D' keys to move within the arena in both perspectives:



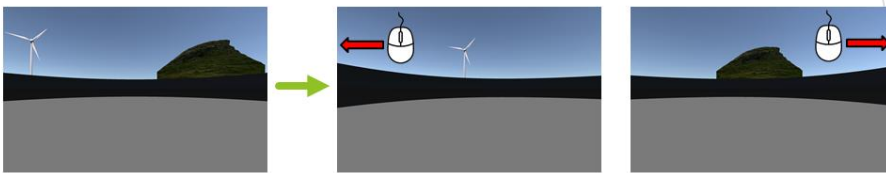
- When you hold these keys, you will initially move slowly but then get faster. You can use this to position yourself more precisely

Next screen: press
'Right Arrow' key

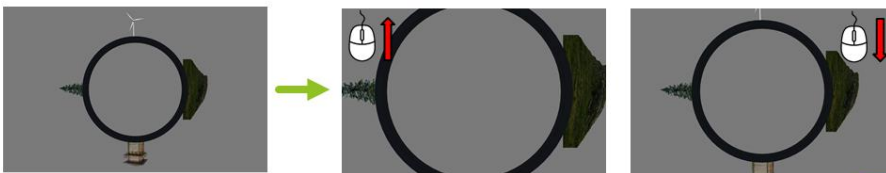
Previous screen: press
'Left Arrow' key

Camera Controls Reminder

- In first person, look left or right by moving the mouse left or right:



- In third person, zoom in and out by moving your mouse forward and backward:



- Press 'Space' once you are ready to practice the Test Phase

Practice Test: press
'Space' key

Previous screen: press
'Left Arrow' key

End of Practice Block

- You have finished practicing a full testing block!
- If you need to take breaks during the testing session, please try to do so only after completing a full testing block like the one you just practiced, otherwise your task performance will be affected
- **Press 'Space' once you are ready to begin the Main Task**

Begin Main Task: press
'Space' key