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**The Impact of Visual Perspective on the Formation
and Retrieval of Memories for Events**

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Thesis submitted for qualification of Doctor of Psychology

University of Sussex

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I hereby declare that this thesis has not been and will not be submitted in whole or in part to another University for the award of any other degree.

Signature:.....

Author Contributions

The thesis was written in a 'paper-style' format. Empirical chapters consist of articles written in a style suitable for publication in peer-reviewed journals, An introduction and general discussion are presented to situate the research within the broader field. I am the principle author on all manuscripts within this thesis and am primarily responsible for design, data collection, analysis, and write-up of each chapter. Dr. Peggy St. Jacques is co-author on the empirical chapters because of her advice at all stages of the research process and expertise within the field. Yoko Lam, an undergraduate student, and Hannah Richards, a Masters in Cognitive Science student, assisted with data collection in the studies in Chapter Four.

Summary

Past events can be recalled either from the perspective of one's own eyes (i.e. first-person perspective) or an observer perspective whereby one is able to visualize oneself inside of the mental scene (i.e. third-person perspective). Visual perspective is a central memory characteristic associated with the type of information recalled and phenomenology during retrieval. However, the majority of neuroimaging studies investigating visual perspective either do not manipulate visual perspective or focus only memories experienced from an own eyes perspective. After reviewing current theory and research on the role of visual perspective in memories for events (Chapter 1), Chapter 2 investigates the spatiotemporal dynamics of networks supporting retrieval of autobiographical events from multiple visual perspectives using a multivariate approach (Partial Least Squares Analysis). Results show that own eyes, relative to observer, perspectives engaged a core autobiographical memory retrieval network to a greater extent during later phases of retrieval. Functional connectivity analyses with an anterior hippocampal seed revealed that own eyes perspectives were also related to increased connectivity with a posterior medial network during the initial construction of autobiographical memories from observer perspectives, and stronger within-MTL connectivity during later retrieval periods from own eyes perspectives.

Together, results suggest that visual perspective is an important factor in understanding how neocortical systems guide memory retrieval.

Having specified neural mechanisms of autobiographical retrieval from multiple visual perspectives, I next turn to how the brain represents memories formed from own eyes and observer perspectives. While events are typically experienced from an own eyes perspective, we are also able to form memories from an observer perspective (e.g.

during events with high levels of self-conscious emotion). Further, how bodily selfhood, more salient in own eyes (i.e. embodied) compared to observer (i.e. disembodied) perspectives, contributes to memory processes is not well understood. In Chapter 3, I employ virtual reality (VR) technology to manipulate perspective while creating realistic, tightly controlled memories to investigate how perspective and embodiment combine to influence patterns of neural activity underlying memory retrieval. Here, perspective was manipulated through the use of a head-mounted display unit linked to a 360° camera. Following a manipulation to alter sense of embodiment and self-location, participants formed memories for neutral events from own eyes and observer perspectives, which were later retrieved during functional scanning. Multivariate pattern analysis revealed key differences in the neural representation of own eyes and observer memories in the angular gyrus and insula, regions crucial to establishing a coherent sense of bodily selfhood and the conscious experience of bodily sensations respectively. In Chapter 4, I continue my investigation of visual perspective during memory formation with two behavioral studies. I developed an immersive virtual reality methodology to manipulate visual perspective in realistic settings by projecting a virtual avatar into different virtual environments experienced from either an own eyes or observer perspective. Results demonstrate an increase in own eyes ratings alongside a decrease in observer ratings over time, suggesting that forming memories from an observer perspective diminishes the strength with which perspective is recalled during retrieval. Limitations and implications for all studies are discussed in Chapter 5.

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Chapter 1 – General Introduction

Autobiographical memory (AM), memory for the personal past, is a complex, dynamic process that must reliably preserve the past while adaptively interpret the present and plan for the future. Visual perspective, that is the particular egocentric viewpoint adopted in a mental scene, is a key example of the flexibility inherent and critical to AM. Moreover, because visual perspective is a rare example of a purely self-specific process (Prebble, Addis, & Tippett, 2014), research devoted to this topic stands to generate novel insights into the role of selfhood in structuring AM. Visual perspective refers to the ability to retrieve AMs from the perspective of one's own eyes (OE; i.e. first-person perspective), or those of an observer (OB) whereby one is able to see oneself in a memory from a bystander's point of view (i.e. third-person perspective; Nigro & Neisser, 1983). While discussion of visual perspective has a long tradition in the psychological literature (e.g. Freud, 1899; Henri & Henri, 1896; Locke, 1971), several critical questions concerning how visual perspective shapes AM remain outstanding. Specifically, relatively little is known about how the brain represents memories from multiple visual perspectives, which is crucial to understanding the flexibility of self-representation which enables AMs to adapt over time. Of equal importance is the investigation of visual perspective during memory encoding. Memories can be formed, not just retrieved, from both OE perspectives, experienced from within the physical body, and OB perspectives,

experienced from outside the body, in healthy (Blackmore, 2017; McCarroll, 2017) and clinical populations (Blanke, Landis, Spinelli, & Seeck, 2004; Koopman, Classen, Cardeña & Spiegel, 1995). Yet, research into how encoding events from an out-of-body perspective affects memory processes at the behavioural, phenomenological, or neural level is scarce. Investigation into visual perspective during memory encoding will reveal unique contributions of embodiment in guiding memories for events, adding to knowledge of how bodily selfhood factors into high level cognitive processes such as memory.

Thus, the main aims of this thesis were to investigate how visual perspective influences the formation and retrieval of memories, ultimately revealing how self-specific processes uniquely shape the way the personal past is remembered. This opening chapter will review (1) theoretical models of visual perspective during AM encoding and retrieval, followed by (2) the behavioural effects and (3) neural correlates of visual perspective in AM. Next, I will consider (4) the role of embodiment in AM and how it relates to the investigation of visual perspective. Lastly, I will (5) summarize the main research aims of the ensuing chapters in this thesis.

1.1. Theoretical Accounts of Visual Perspective in AM

1.1.1. Memory Formation

The vast majority of previous research on visual perspective has assumed that memories in healthy individuals are strictly encoded from an OE perspective (e.g. Butler, Rice, Woolridge, & Rubin, 2016; De Brigard, 2014), and that encoding from an OB perspective is only the case in the clinical contexts of dissociation

(Koopman et al., 1995), schizophrenia, depression, anxiety (Blanke, Landis, Spinelli, & Seeck, 2004), and neurological damage (Blanke & Mohr, 2005). Consequently, OB perspectives tend to be construed as examples of memory distortion, due to a mismatch between the way an event was experienced and the way it is subsequently recalled. In other words, since events are assumed to only be encoded from an OE perspective, OB perspectives must be based on information that was not present at the time of the original event and, thus, distorted (De Brigard, 2014; Fernández, 2015).

However, Nigro & Neisser's (1983) seminal paper representing the first empirical investigation of visual perspective clearly states that while memories are typically formed from an own eyes perspective, "it is also possible to have observer experiences ... [whereby] we are conscious of how the entire scene would appear (or does appear in fact) to an onlooker who sees us as well as our surroundings" (p. 468). These OB perspective experiences in turn create OB memories (i.e. memories for events encoded from an OB perspective). In support of the concept of OB memories, observer perspective experiences are described as "normal, though unusual event(s)" (p. 163, Amorim, 2003), prevalent in 15% of the general population (Blackmore, 2017).

Certain factors present during memory formation can create OB perspective experiences (McCarroll, 2017; Nigro & Neisser, 1983). Specifically, Nigro and Neisser (1983) observed that events involving high levels of self-conscious emotion where one is aware of being observed or evaluated (e.g. public speaking), not only tend to be retrieved from OB perspectives, but also promote detachment

from the situation as it is unfolding (Nigro & Neisser, 1983). This detachment can subsequently lead to OB perspective mental imagery as the event is experienced (Rice, 2010), leading to OB perspective experiences during memory formation (McCarroll, 2017). Traumatic events constitute another example of situations that enable OB perspective mental imagery as an event is experienced. Mclsaac and Eich (2004) found that nearly 40% of participants who had undergone traumatic events reported experiencing the event from an OB perspective as it was occurring. A separate study by Cooper, Yuille, & Kennedy (2002) investigated visual perspective at encoding by asking participants “Were there moments when you felt as though you were a spectator watching what was happening to you – for example, did you feel as if you were floating above the scene or observing as an outsider?” (p. 84) as they recalled memories for positive events, a sexual assault, and a non-sexual trauma. The authors found that participants reported a greater number of OB perspective experiences for the non-sexual traumatic events and endorsed the possibility for individuals to experience events from both OE and OB perspectives. While these investigations rely on retrospective reports, which preclude verification, they do point to a strong likelihood for events to be encoded from both OE and OB perspectives (McCarroll, 2017). Lastly, individual, as well as situational, factors also enable OB perspective experiences. For example, individuals with social phobia who possess high levels of self-awareness commonly report observer perspective experiences (Clark, 2001), amplified in social contexts laden with anxiety (Wells & Papagerogiou, 1999).

In sum, while the vast majority of research has tended to assume that events are encoded only from an OE perspective, Nigro & Neisser (1983) and McCarroll (2017) have emphasized the strong possibility of encoding events from OB perspectives, depending on situational and individual characteristics. What remains to be determined is how OB perspective experiences influence memory at the behavioral and neural level, which will be addressed in Chapters 2 and 3 of this thesis. Having specified current thinking on the role of visual perspective in AM formation, I now turn to theoretical accounts of how OE and OB perspectives contribute to AM retrieval processes.

1.1.2. Memory Retrieval

Theoretical models of visual perspective in AM retrieval have focused on its role in establishing a coherent yet dynamic sense of self. For example, Libby and Eibach (2011) claim that visual perspective functions as a tool to represent the self in multiple ways by extracting an event's meaning at two different levels. To frame their theory, the authors draw on discussions of the dual-faceted nature of self. The self is comprised of two main components: an "I" rooted in moment-to-moment sensory experience perceived in a bottom-up fashion, and a "me" that represents the self as an abstract, conceptual object that persists across time (Damasio, 1994; Epstein, 2003; Gallagher, 2000; James, 1890/1950, LeDoux, 2003; Wilson, 2002). Adopting an OE perspective in AM emphasizes the experiential facet of the self by framing events in terms of its tangible, sensory features (Libby & Eibach, 2001). In contrast, adopting an OB perspective in AM integrates an event within the broader context of one's life, framing it in terms of its abstract meaning and incorporating

information not present in the original event (Libby and Eibach, 2011). Evidence of this theory of visual perspective as a representational tool to understand the self stems from a study that asked undergraduate students to describe a past event (i.e. high school graduation) either in terms of the event's concrete details, such as physical actions and bodily sensations, or in terms of how the event connected to other AMs and the individual's broader self-identity (Libby, Valenti, Hines, & Eibach, 2011). Construing an event in terms of its wider context led to the adoption of an OB perspective in memory. The same pattern was observed when picturing an imagined future event (i.e. college graduation), demonstrating a high degree of overlap between cognitive processes employed in retrieving an AM and mental imagery. Further support for the theory of visual perspective as a representational tool (Libby & Eibach, 2011) comes from a separate study that asked participants to imagine helping a friend cheat on an exam after learning either that their friend had just been romantically rejected (i.e. was too emotionally distraught to properly prepare) or purchased a new television (i.e. was not disciplined enough to properly prepare; Valenti & MacGregor, 2011). Participants then rated how immoral it was to help their friend cheat. Supporting the idea that observer perspectives cast an event's meaning in terms of its broader context, participants rated their actions as less immoral in the romantic rejection compared to new television condition only when an observer perspective was adopted. Own eyes perspectives did not have an effect on immorality judgements, showing that they are not influenced by an event's wider context. Thus, visual perspective defines the level of meaning with which an AM is understood; OE perspectives construe past (and imagined) events

in terms of bottom-up sensory components tied to a specific point in time, whereas OB perspectives trigger a top-down approach that takes into account knowledge and experience external to the original event.

This approach differs from previous theoretical models that have assumed OB perspectives in AM consistently distance an individual from his/her past self by reducing reliving and emotional intensity, thereby protecting against harmful negative self-views (e.g. Holmes & Mathews, 2010; Kenny et al., 2009; Williams & Moulds, 2007). Critically, Libby and Eibach's (2011) model emphasizes that while OB perspectives have the potential to perform a self-distancing function, they may also highlight similarities between past and present selves to establish a sense of self-continuity, depending on an individual's motivational goals at the time of retrieval. To demonstrate the ability of OB perspectives to perform both self-distancing and self-continuity functions depending on personal motivations, Libby, Eibach, and Gilovich (2005) asked undergraduate participants to retrieve an AM from their time in high school while either focusing on aspects of themselves that had changed or remained stable since the time of the event. OB perspectives resulted in greater ratings of self-distancing if participants were told to focus on differences between past and present selves, but greater ratings of self-continuity if asked to focus on similarities between past and present selves. In contrast, retrieving AMs from an OE perspective did not influence ratings of self-change, consistent with the authors' theory that only observer perspectives are capable of shaping the abstract, broader meaning of events. Thus, Libby and Eibach (2011) have highlighted how OB perspectives should not be understood only as a means

to distance past from present selves, but rather as a flexible representational tool used to derive an abstract level of meaning from an AM.

Sutin and Robins (2008) also emphasize the ability of OB perspectives to fulfill different self-evaluative functions by contrasting a Dispassionate Observer against a Salient Self account of visual perspective in AM retrieval. In the Dispassionate Observer account, observer perspectives in AM distance past from present selves by reducing the reliving and emotional intensity of retrieved events, thereby facilitating an objective view of the self that provide a buffer against negative self-evaluations (Sutin & Robins, 2008). For example, when an individual retrieves an AM incongruent with or psychologically threatening to the current self, thereby posing a threat to a stable self-concept, OB perspectives will distance past from present selves in order to maintain self-continuity and a positive self-concept. However, Sutin and Robins (2008) also suggest that OB perspectives may instead increase the level of self-focused attention during AM retrieval, consequently enhancing emotions associated with the event and fostering strong connections between different iterations of the self over time. According to this Salient Self account of visual perspective, when an individual retrieves an AM wherein the past self is congruent with the present self, OB perspectives will increase self-continuity and emotional intensity. Similar to Libby and Eibach's (2011) theory, Sutin and Robins (2008) also make clear that an individual's personal motivations (e.g. whether the goal of retrieval is self-continuity or self-distancing) will determine how visual perspective affects AM retrieval.

In sum, theoretical accounts of visual perspective have focused on self-evaluative functions of AM retrieval. Libby and Eibach (2011) highlight how OE and OB perspectives are used as a tool to represent the self in different ways. OE perspectives cue a bottom-up processing style in which concrete and sensory details dominate retrieval, construing the self as an experiencing “I” locked into specific moments and sensory experiences in time. In contrast, OB perspectives employ a top-down processing style whereby the self is understood as an object within the external world, or conceptual “me”, by integrating a retrieved AM within a broader context of past experience, thereby endowing the event with abstract meaning. Sutin and Robins (2008) have also emphasized the flexible functioning of visual perspective in AM with their model that includes both Dispassionate Observer, where OB perspectives serve a self-distancing function, and Salient Self views, where OB perspectives enhance self-continuity. Critically, both models emphasize how an individual’s motivation at the time of retrieval will determine the effect of visual perspective on AM. Having established a theoretical foundation for the role of visual perspective in AM, I now turn to research demonstrating its impact at retrieval on memory content, phenomenology, and accuracy.

1.2. Effects of Visual Perspective on AM Content, Phenomenology, and Accuracy

OE and OB perspectives are distinctly linked to specific biases in the type of information recalled during AM retrieval. For example, OE perspectives are more likely to be adopted when individuals are asked to focus on subjective feeling states accompanying AM retrieval (D’Argembeau, Comblain & Van der Line, 2003;

Nigro & Neisser, 1983). In contrast, emphasis on concrete, contextual details of an AM result in the adoption of OB perspectives (Nigro & Neisser, 1983).

Demonstrating that visual perspective directly determines the type of memory content retrieved, adoption of own eyes perspectives directs attention inwards to emotional, bodily, and psychological states in memory narratives, whereas adoption of OB perspectives emphasizes external aspects of a mental scene, such as the physical appearance of individuals within the memory, their specific actions, and the spatial layout of the environment (Mclsaac & Eich, 2002). In a separate study that asked participants to retrieve details from memory after listening to verbally presented passages, own eyes perspectives again resulted in enhanced retrieval of internal sensory, emotional, and psychological states (Bagri & Jones, 2009). Although OB perspectives were not associated with an increased focus on objective, contextual details as reported by Mclsaac and Eich (2002), this is likely due to methodological dissimilarities pertaining to differences in memory for verbal material versus realistic, complex events.

Biases in the content of information in AMs according to visual perspective influence the phenomenology of retrieval, that is the way in which an AM is subjectively re-experienced. As noted, OE perspectives tend to be associated with emotional as opposed to neutral memories (D'Argembeau et al., 2003; Nigro & Neisser, 1983). Moreover, switching from an OE to OB perspective reduces the emotional intensity associated with AM retrieval, alongside decreases in sensory detail and reliving (Bernsten & Rubin, 2006). Further, Sutin & Robins (2010) demonstrated that adoption of OE perspectives results in increased vividness and

coherence within AMs, in addition to previously reported heightened sensory information.

However, Libby & Eibach (2011) make clear that OB perspectives are not always associated with reductions in the subjective re-experiencing of events at retrieval. Rather, an individual's motivational state will determine the influence of visual perspectives on memory processes. Specifically, if higher levels of emotion are elicited by picturing an event's meaning in the wider context of one's life compared to its experiential details, then OB perspectives will increase emotional intensity whereas OE perspectives will dampen it (Libby & Eibach, 2011). An example of the ability for OB perspectives to heighten emotional intensity within event memories relates to feelings of regret (Libby & Eibach, 2011). Regret tends to be higher for actions (e.g. asking out a love interest, but being rejected) compared to inactions (e.g. not having the courage to ask out a love interest, and always wondering whether s/he would have said yes; Gilovich & Medvec, 1995). Steps can be taken to minimize the negative emotions that arise from regrettable actions allowing one to move on from the experience, whereas regrettable inactions force an individual to consider the myriad ways life could have changed if they had only behaved differently, making the resolution of negative emotions more difficult (Gilovich & Medvec, 1995). With this research in mind, Valenti, Libby, and Eibach (2011) had participants retrieve AMs associated with regretful actions or inactions from either an OE or OB perspective. Adoption of OB perspectives decreased regret for past regretful actions, but increased feelings of regret during the retrieval of events associated with regretful inactions. In contrast, OE

perspectives did not influence perceived regret. Findings are again consistent with the theory that OB perspectives prompt an individual to consider an AM within its wider context. Namely, during the retrieval of both regretted inactions and actions, participants cast the event in terms of its broader meaning. For regretted actions, OB perspectives allowed participants to see how the event, though embarrassing at the time, did not in fact have a large, negative impact on the course of their overall lives, reducing the emotional intensity of retrieval. For regretted inactions, OB perspectives highlighted how participants' lives may have changed if only they had behaved differently, thereby increasing the emotional intensity of retrieval.

In a further demonstration of the capacity for OB perspectives to heighten emotional intensity of pictured events, Libby, Shaeffer, Eibach, and Slemmer (2007a) asked participants to imagine themselves voting in an approaching election from either an OE or OB perspective and rate how enthusiastic they felt about voting. The authors found that observer perspective imagery, which led participants to consider the act of voting within the context of their personal identities and past experiences more so than own eyes perspective imagery, led to greater excitement and reduced apathy for voting. Consequently, the increased voter enthusiasm associated with observer perspective imagery resulted in a stronger commitment to casting a ballot (Libby et al., 2007a) and even higher voter turn-out rates in the actual election (Libby, Shaeffer, Eibach, & Slemmer, 2007b). Importantly, these two studies reveal that differences in phenomenology according to visual perspective mediate effects on an individual's subsequent behaviour,

thereby demonstrating the pivotal role visual perspective plays in using memory and mental imagery to guide interactions with the external world.

Effects of visual perspective on phenomenology have recently been shown to impact objective memory accuracy. Marcotti and St. Jacques (2018) had participants encode a series of lab-based events experienced from an OE perspective, which were later retrieved from either an OE or shifted OB perspective. Memory accuracy was then assessed with cued recall questions pertaining to specific sensory, visual, and spatial details of the events. Results across two experiments revealed that switching to an OB perspective led to reductions in vividness during retrieval, which in turn predicted diminished memory accuracy. This study was the first to demonstrate that visual perspective modulates long-term objective memory precision.

Hence, visual perspective biases access to different types of information (i.e. experiential vs. contextual) during retrieval, which impacts how a memory is subjectively re-experienced, subsequent behaviour, and objective memory accuracy. Having reviewed the influence of visual perspective on behavioural and phenomenological aspects of AMs grounded within a theoretical context, I now turn to how the brain represents memories retrieved from different visual perspectives.

1.3. Neural Correlates of Visual Perspective in AM Retrieval

While several studies over the last few decades have yielded a comprehensive understanding of visual perspective influences the behavioral correlates of AM retrieval, much less is known about the underlying neural mechanisms. One reason is that visual perspective is frequently left uncontrolled or

restricted to an OE perspective in functional neuroimaging studies of AM. This may explain why the precuneus is not considered to be a core region during AM (for review see Svoboda, McKinnon, & Levine., 2006), despite robust recruitment in nearby posterior cingulate regions. Those AM studies that have reported precuneus have linked neural recruitment to the ability to generate and elaborate upon vivid mental images (Daselaar et al., 2008; Fuentemilla, Barnes, Düzel, & Levine, 2014; Gardini, Cornoldi, De Beni, & Venneri., 2006; Söderlund et al., 2012), as well as the construction of complex and realistic scenes (Hassabis, Kumaran, & Maguire, 2007; Summerfield, Hassabis, & Maguire., 2009).

Recently a handful of studies have directly investigated visual perspective during AM retrieval, but they have found inconsistent findings related to the involvement of posterior parietal cortices. Structural MRI studies have suggested that the volume of grey matter in the precuneus is positively related to the spontaneous retrieval of AMs from an OE perspective (Freton et al., 2014; Hebscher, Levine, & Gilboa, 2018). However, fMRI studies have reported greater recruitment of the precuneus for OB perspectives (Grol, Vingerhoets, & De Raedt; 2017) or common involvement (Eich, Nelson, Leghari, & Handy, 2009). In a recent fMRI study, Iriye and St. Jacques (2018) found that the involvement of posterior parietal cortices depended upon how and when these regions interact with the hippocampus. During early phases of retrieval, when a particular memory was searched for and initially constructed, OB perspectives were associated with stronger hippocampal functional connectivity with posterior parietal regions (i.e., precuneus, angular gyrus), and subsequently led to less recruitment of posterior

parietal and other core AM regions during later phases of retrieval when memory details were elaborated upon.

The inconsistent findings regarding the involvement of posterior parietal cortices when adopting a particular egocentric perspective during memory retrieval could be explained by differing demands related to shifting visual perspective. Supporting this idea, St. Jacques, Szupunar, and Schacter (2017) recently demonstrated involvement of the posterior parietal cortex (i.e., precuneus and angular gyrus) when participants were asked to actively shift their visual perspective during AM retrieval from a dominant OE perspective to an OB perspective. Moreover, they found that the degree of precuneus involvement when shifting visual perspective also predicted the degree of online reductions in emotional intensity during retrieval, as well as subsequent changes in the dominant visual perspective of AMs. Subsequent research has replicated this finding, demonstrating increased involvement of the precuneus when shifting visual perspective—regardless of the direction of the shift in perspective (St. Jacques, Carpenter, Szupunar, & Schacter, 2018). These findings dovetail with theories of memory and imagination that suggest that egocentric frameworks generated during retrieval from long term memory within the precuneus can be manipulated and updated when people imagine the possible movements they can make within the remembered scene (Byrne, Becker, & Burgess, 2007). Such processes may be recruited more when people adopt an OB perspective during retrieval, which is more likely to require updating internal representations of the world in order to retrieve memories from a novel self-location in space. Interestingly, recent fMRI

research has also shown that the manipulation of egocentric perspective during AM retrieval is associated with neural recruitment in some of the same brain regions that are typically more involved in the constructive processes that support imagination (St. Jacques et al., 2018).

Altogether, this section has summarized current thinking on the theoretical, behavioral, phenomenological, and neural implications of visual perspective in AM. However, a comprehensive understanding of visual perspective is not complete without a consideration of how embodiment (i.e. the feeling of being physically located within one's body) impacts AM processes. OE perspectives are necessarily retrieved from within the body, while OB perspectives are defined by a vantage point located outside the body. Yet, how visual perspective and embodiment interact to influence AM is not well understood. A theoretical and empirical framework for understanding this relationship will elucidate mechanisms by which self-specific processes, of which visual perspective and embodiment are two prime examples, guide memories for the personal past, ultimately shaping interpretation of the present and behavior in the future.

1.4. The Role of Embodiment in AM

Embodiment plays a key role in memories of the personal past (for review see Dijkstra & Post, 2015). AM retrieval necessarily involves the reactivation of stored sensory, motor, and affective information physically experienced at the time of the original event (Wilson, 2002), leading to the conclusion that AMs are inherently spread throughout the body and brain and resulting in an embodied memory trace (Damasio, 1999; Glenberg, 1997). This robust memory trace replete with sensory,

motor, affective, as well as contextual information renders it resistant to forgetting, allowing the event to be vividly re-experienced when it is later retrieved (Dijkstra, Kaschak, & Zwann, 2007).

The role of embodiment in AM is evident in finding that matching a body posture assumed during the original experiencing of an event at retrieval facilitates memory access and results in stronger memory retention over time (Dijkstra et al., 2007). Participants were cued to retrieve a series of AMs characterized by specific body postures (e.g. undergoing a dental procedure) while in a position either congruent (e.g. lying in a reclined position) or incongruent (e.g. standing upright with hands on hips) with the event. Reaction times to access a relevant AM were faster if retrieved from a congruent body position. Moreover, AMs associated with congruent body postures were spontaneously recalled more frequently during a follow-up testing session two weeks later, compared to AMs associated with incongruent postures. Interestingly, this effect was stronger in younger compared to older participants, which the authors' attributed to the fact that younger participants reported higher reliving during retrieval. Thus, the incorporation of embodied (i.e. sensory, motor, and affective) information into a memory trace supports its subsequent retrieval by allowing the event to be vividly re-experienced. The more the event is re-lived, the stronger the facilitatory effects on AM retrieval.

In addition to body postures, body movement has been shown to influence AM retrieval. Certain actions trigger specific synesthetic emotional associations. For example, upwards movements are linked with positive affect while downwards movements are connected to affect (Dijkstra, Eerland, Zijlmans, & Post, 2014).

Making use of this natural association between body movements and emotion, Cassanto and Dijkstra (2010) cued participants to retrieve either positive memories associated with pride or negative memories associated with shame while participants were asked to place marbles held in each hand in a high or low container. Participants were faster to retrieve AMs when the direction of the hand movements matched the valence of the memory (i.e. when positive memories were retrieved while making upwards hand movements, or when negative memories were retrieved while making downwards movements). In a subsequent experiment where participants were prompted with a neutral cue (i.e. tell me of an event that happened yesterday), participants were more likely to recall positively valenced AMs when upwards hand movements were made, and negatively valenced AMs when downwards hand movements were made. Together, findings demonstrate the facilitatory effect of body motion (Cassanto & Dijkstra's, 2010; Dijkstra, Kaschak, & Zwann, 2007) in accessing AMs.

Evidence of the role of embodiment in memory is also present in the brain, and simultaneously identifies visual perspective as an important factor in guiding retrieval. For example, Eich and colleagues (2009) found that the retrieval of complex lab-based events during functional scanning from an OB perspective is associated with decreased activation of regions representing bodily selfhood, including somatosensory, motor, and insular cortices (Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004; Critchley, Mathias, & Dolan, 2001). In contrast, adoption of OE perspectives leads to increased activation of the amygdala, which underlies the regulation of affective reactions deeply rooted in bodily reactions to emotional

stimuli (Eich, et al.,2009). Moreover, Grol and colleagues (2017) observed neural recruitment of the temporal parietal junction (TPJ) was greater after adopting an OB perspective compared to an OE perspective during AM retrieval. Supported by evidence of the TPJ's involvement in own-body mental imagery (Arzy et al., 2006; Blanke & Arzy, 2005), the authors related the observed TPJ activity to the performance of own-body-transformations required to mentally shift egocentric perspective to a disembodied self-location. Thus, adopting OB perspectives during memory retrieval is linked to reduced activation of areas associated with bodily sensations (i.e. insular and somatomotor cortices; Eich,et al., 2009) alongside increased recruitment of areas that mediate mental imagery of one's own body (i.e. TPJ; Grol et al.,2017).

Lending novel insight into the influence of embodiment and visual perspective during memory formation, Bergouignan, Nyberg, and Ehrsson (2014) investigated how encoding realistic events from a first-person perspective centered within the body versus outside of the body influenced how memories were later remembered. Participants experienced a realistic social interaction while wearing a virtual reality headset live-linked to a 360-degree camera positioned to create a first-person perspective within or outside of the body, and the sense of embodiment was manipulated using visuo-tactile feedback. They found that memories encoded from an out-of-body perspective were associated with a decrease in recollection and changes in recruitment of the posterior hippocampus, when compared to memories encoded from within the body. This preliminary study provides initial insight into

how embodiment during memory formation influences the interaction between visual perspective and AM retrieval.

In sum, AMs are by nature embodied because the sensory, motor, and affective components of the original event are vividly re-experienced during retrieval, leading to a widely distributed memory trace (Damasio, 1999; Glenberg, 1997). The embodied nature of memory has been shown both behaviourally (Dijkstra et al., 2007) and in the brain (Bergouignan et al., 2014; Eich et al., 2009; Grol et al., 2017). Crucially, existing neuroimaging studies suggest that embodiment is more strongly represented in events experienced from an own eyes perspective (i.e. Eich et al., 2009), whereas observer perspectives are associated more with own-body mental imagery (i.e. Grol et al., 2017), which influences how critical hubs of system like the hippocampus direct memory processes (i.e. Bergouignan et al., 2014). However, only a handful of studies have investigated the relationship between embodiment, visual perspective, and memory, and several key questions concerning how self-specific processes underpin memory remain. These will be the focus of chapter four. First, I will outline the main aims of this thesis in the next section.

1.5. Aims

This thesis aims to understand how visual perspective influences the behavioral and neural mechanisms underlying AMs. How visual perspective is represented in the brain has only been investigated by a handful of neuroimaging studies, yet, an in-depth understanding of its neural correlates is necessary to a comprehensive account of AM. For example, a significant gap in our knowledge of AM is that the

majority of studies of AM either do not manipulate visual perspective or have only investigated memories retrieved from an OE perspective. Thus, it is currently unknown whether visual perspective shapes memories by modifying how a specific memory is initially searched for and constructed or by biasing the subsequent elaboration of details within memories. The first goal of this thesis was to investigate how explicitly manipulating visual perspective influences the neural mechanisms associated with remembering personal past events using a multivariate approach. In Chapter 2, I investigated the underlying mechanisms of visual perspective by asking participants to adopt specific visual perspectives as they retrieved AMs cued by familiar spatial locations during functional scanning. The initial phase of retrieval, characterized by memory construction, was dissociated from a subsequent memory elaboration by asking participants to press a button when a unique memory associated with the familiar location was firmly in mind, after which the details of the memory were embellished upon for the remainder of the trial period.

However, visual perspective varies during memory formation, as well as retrieval (Nigro & Neisser, 1983; McCarroll, 2017). Yet, very little research has been devoted to understanding how OE and OB perspectives during memory formation influence subsequent memory retrieval, partly due to technological limitations in manipulating perspective during lived experience. In Chapter 3, I investigate how visual perspective at encoding influences the neural mechanisms of retrieval. This chapter further examines how embodiment interacts with visual perspective to influence patterns of neural activity during memory retrieval.

Participants underwent a manipulation to alter their sense of bodily self-location while wearing an Oculus Rift head-mounted display (HMD), then formed memories for a series of everyday events. In a separate session occurring on the same day, participants were asked to retrieve these newly formed memories during functional scanning to elucidate neural differences between memories encoded from within and outside the physical body.

In Chapter 4, across two behavioral studies, I capitalize on recent advances in VR technology that allow for the manipulation of visual perspective during memory formation in realistic, yet tightly controlled virtual environments to investigate effects on objective memory accuracy and subjective phenomenology during retrieval. The first of these studies had participants visually explore virtual environments while wearing an Oculus Rift HMD from either an OE or OB perspective using assigned virtual avatars, followed by an assessments of visual memory accuracy, spatial memory accuracy, and phenomenological memory properties immediately following encoding. The second study builds upon the methods of the previous study through increasing the level of immersion within virtual environments by including motion capture, strengthening self-identification with the avatar through the use of bespoke avatars tailored to each participant's appearance, and including a delayed testing point one week following the initial encoding session to assess effects of visual perspective on memory over time.

Together, these studies offer unique contributions to research on how visual perspectives shapes memories at both neural and behavioral levels. Better understanding of the mechanisms that support the fundamental capacity to

understand ourselves from multiple perspectives lends insight into how a stable, yet flexible, sense of self is created and maintained over time through memory.

Chapter 2. Construction and Elaboration of Autobiographical Memories from Multiple Visual Perspectives

2.1. Abstract

Visual perspective is a fundamental aspect of autobiographical memory. Yet, exactly how visual perspective influences the functional mechanisms supporting retrieval is unclear. Here we used a multivariate analysis to characterize the spatiotemporal dynamics of networks supporting autobiographical memory retrieval from multiple visual perspectives. Both OE and OB perspectives engaged an autobiographical memory retrieval network (i.e., hippocampus, anterior and posterior midline, lateral frontal, and posterior cortices) that peaked during later retrieval periods, but was recruited less strongly for OB perspectives. Functional connectivity analyses with an anterior hippocampal seed revealed that visual perspective was also linked with alterations in the strength and timing of neural recruitment. There was stronger hippocampal connectivity with a posterior medial network and ventromedial prefrontal cortex during the initial construction of autobiographical memories from OB perspectives and stronger within-MTL connectivity during later retrieval periods from OE perspectives. Findings demonstrate that adopting OE and OB perspectives during autobiographical memory retrieval are associated with distinct patterns of hippocampal-neocortical interactions associated with differential recruitment of the autobiographical memory retrieval network during later retrieval periods, thereby supporting the central role of visual perspective in reconstructing the personal past.

2.2. Introduction

Autobiographical memory retrieval requires taking a particular egocentric perspective, or window on which to remember the past. Autobiographical memories can be retrieved from an own eyes (OE) or multiple observer (OB) vantage points, and the particular visual perspective adopted shapes the content and phenomenology of autobiographical memories (e.g., Berntsen & Rubin, 2006; Butler, Rice, Woolridge, & Rubin, 2016; Mclsaac & Eich, 2002; Marcotti & St. Jacques, 2017; Nigro & Neisser, 1983; Rice & Rubin, 2009). Previous functional neuroimaging studies have indicated that autobiographical memory retrieval is associated with neural recruitment in anterior and posterior midline regions, medial temporal lobe (MTL), and frontoparietal regions that overlap with the default network (e.g., Kim, 2012; St. Jacques, Kragel, & Rubin., 2011; for recent review see Andrews-Hanna, Saxe, & Yarkoni., 2015). Moreover, this research has shown that the pattern of functional recruitment and functional interactions within these regions varies across the construction and elaboration phases of autobiographical memory retrieval (e.g., Addis, Wong, & Schacter., 2007; Daselaar et al., 2008; Inman, James, Vytal, & Hamann, 2018; McCormick, St-Laurent, Ty, Valiante, & McAndrews, 2015; St. Jacques et al., 2011).

A significant gap in our understanding, however, is that the majority of studies of autobiographical memory either do not manipulate visual perspective or

have focused solely on memories retrieved from an OE perspective. Thus, it is currently unknown whether visual perspective shapes memories by modifying how a specific memory is initially searched for and constructed or by biasing the subsequent elaboration of details within memories. Moreover, while there are several possible OB perspectives that can be adopted within a mental scene, some more common than others (Rice & Rubin, 2011), how these different alternatives influence the neural mechanisms of autobiographical retrieval is not yet understood. Here, we take a multivariate fMRI analysis approach to investigate the influence of multiple visual perspectives on functional neural recruitment and functional connectivity across the time-course of autobiographical memory retrieval.

A growing number of neuroimaging studies have begun to investigate visual perspective during long-term memory retrieval (Fretton et al., 2014; Grol et al., 2017; Hebscher et al., 2018; St. Jacques et al., 2018; 2017; also see St. Jacques et al., 2013). Structural neuroimaging studies have shown a positive relationship between precuneus volume and the tendency to adopt an OE perspective during autobiographical retrieval (Fretton et al., 2014; Hebscher, Levine, & Gilboa, 2018). However, functional neuroimaging studies are less consistent—with some studies finding similar involvement for OE and OB perspectives (Eich, Nelson, Leghari, & Handy, 2009; St. Jacques, Carpenter, Szpunar, & Schacter, 2018) and others finding greater involvement for OB than OE perspectives (Grol, Vingerhoets, & de Raedt, 2017). One reason for this inconsistency may be that the precuneus is involved in both the representation and manipulation of mental images that support

the adoption of OE and OB perspectives alike (for review see Byrne, Becker, & Burgess, 2007; Cavanna & Trimble 2006). Supporting this viewpoint, St. Jacques and colleagues (2018) and St. Jacques, Szpunar, & Schacter (2017) demonstrated that the precuneus contributes to the ability to shift to alternative visual perspectives—irrespective of the direction of perspective shifting.

Visual perspective also influences neural recruitment in regions associated with bodily self-representation and emotional response, consistent with reports of heightened physical sensations and emotional intensity that accompany retrieval from an OE perspective (e.g. Berntsen & Rubin, 2006; McIsaac & Eich, 2002). For example, Eich and colleagues (2009) asked participants to retrieve memories for complex lab-based events and found increased involvement of amygdala for memories retrieved from OE perspectives, which they linked to behavioral decreases in affect, and reduced activation of somatomotor and insular cortices for OB perspectives, attributed to diminished physical sensations during retrieval.

Visual perspective may also influence functional recruitment of the hippocampus and the integrity of its network connections. Retrieving memories encoded from OE compared to OB perspectives alters neural recruitment of the hippocampus during remembering (Bergouignan, Nyberg, & Ehrsson, 2014), and higher OE ratings during autobiographical memory retrieval are associated with greater engagement of an MTL network centered on the hippocampus (St. Jacques, Kragel, & Rubin, 2013). However, previous research has not delineated how explicitly manipulating visual perspective on a trial-by-trial basis influences the time course of autobiographical memory retrieval.

Construction and elaboration of autobiographical memories involve dissociable neural mechanisms (Addis, et al., 2007; Daselaar et al. 2008; Inman et al., 2018; St. Jacques et al., 2011), which may be differentially affected by visual perspective. On the one hand, visual perspective may influence autobiographical memory retrieval early on during the construction period, because perspective is tightly linked to self-referential processes associated with the medial prefrontal cortex (PFC; e.g., D'Argembeau et al., 2013) that emerge early during the time course of event retrieval and initiate neural recruitment in a widespread network, including the hippocampus (McCormick et al., 2015; St. Jacques et al., 2011). Additionally, manipulating visual perspective during autobiographical memory retrieval involves similar constructive demands as those that support episodic simulation (St. Jacques et al., 2018), which rely on frontoparietal regions (for meta-analysis see Benoit & Schacter 2015), and these constructive processes tend to emerge earlier rather than later during episodic simulation (e.g., Addis et al., 2007). Finally, emotional intensity, which is influenced by visual perspective during autobiographical memory retrieval (e.g., Berntsen & Rubin 2006), modulates neural recruitment in the amygdala and hippocampus early during the initial period of retrieval (Daselaar et al., 2008). On the other hand, visual perspective may predominately influence later elaboration of autobiographical memories, when sensory and perceptual aspects of memories are re-experienced (Conway & Pleydell-Pearce 2000). Visual perspective is supported by mental imagery processes linked to the precuneus and visual cortices (for review see Cavanna & Trimble 2006; Pearson, Naselaris, Holmes, & Kosslyn, 2015), that emerge during

the later elaboration of memories (Conway, Pleydell-Pearce, & Whitecross; Daselaar et al., 2008; McCormick et al., 2015). Moreover, during elaboration there is also heightened functional connectivity between the precuneus and posterior visual cortices (Inman et al., 2018), and bilateral posterior hippocampus and visual cortices (McCormick et al., 2015). Alternatively, visual perspective could influence both phases of autobiographical retrieval. For example, St. Jacques, Kragel, & Rubin (2013) showed that people who had higher OE ratings during AM retrieval recruited the MTL network more throughout construction and elaboration periods of retrieval.

While several fMRI studies have investigated differences between construction and elaboration of autobiographical memories during retrieval (e.g., Addis et al., 2007; Daselaar et al., 2007; St. Jacques et al., 2011), *when* precisely visual perspective affects retrieval has yet to be determined. Thus, it is unknown whether visual perspective influences how autobiographical memories are initially selected or, alternatively, how specific memory details are elaborated upon during later phases of retrieval. The present fMRI study examined how explicitly manipulating visual perspective during autobiographical memory retrieval influences the neural mechanisms associated with construction and elaboration of memories. Participants retrieved autobiographical memories from a specified OE or OB perspective elicited by familiar location cues, or completed a control condition involving spatial visualization without retrieving a specific autobiographical memory. I also manipulated the typicality of perspective to better understand the variety of possible OB perspectives that can be adopted in an

autobiographical memory, which was determined by previous findings (Blackmore 1987; Rice & Rubin, 2011).

A multivariate analytical approach, partial least squares (PLS; Addis, McIntosh, Moscovitch, Crawley, & McAndrews., 2004; Burianova, McIntosh, & Grady., 2010; Lin et al., 2003), was employed to examine task-related differences in patterns of brain activity. To determine the degree to which subjective aspects of retrieval accounted for observed effects, additional behavioral PLS analyses were conducted on reaction times to construct an autobiographical memory or spatial visualization and subjective ratings of vividness, perspective maintenance, and emotional intensity collected in-scanner.

Additionally, I conducted a PLS connectivity analysis on the hippocampus because functional integration with this region has been shown to differ across construction and elaboration phases of autobiographical retrieval (McCormick et al., 2015), and is also influenced by visual perspective (St. Jacques et al., 2011). PLS was specifically selected for its ability to characterize task-related differences at specific time points during autobiographical memory retrieval in order to distinguish early (i.e., construction) from later (i.e., elaboration) retrieval periods. Such multivariate techniques have the advantage of increased sensitivity to effects compared to univariate analyses (e.g., Haxby, 2012). For example, while Addis and colleagues (2004) identified regions differentially activated by general versus specific autobiographical memories using traditional univariate techniques, only a PLS analysis was able to uncover a common network including a key connection to the hippocampus. An additional advantage is the elimination of the need to correct for

multiple comparisons, as all computations are carried out in a single analytic step, resulting in more accurate statistical images (Lin et al., 2003; McIntosh & Lobaugh 2004).

The main aims of the study were to determine whether visual perspective predominately modulates how autobiographical memories are searched for and constructed or how memory details are elaborated on during later stages of retrieval, in terms of neural recruitment and hippocampal-neocortical interactions. Based on the link between visual perspective and mental imagery processes that tend to occur later during elaboration of AMs (Daselaar et al., 2008), we predicted that visual perspective would primarily influence later periods of AM retrieval, as reflected by greater differences in the pattern of neural activity for AMs retrieved from OE and OB perspectives during later time periods. Additionally, given evidence that visual perspective influences engagement of MTL networks that contribute to AM retrieval across both construction and elaboration phases (St. Jacques et al., 2013), I predicted that visual perspective would influence hippocampal-connectivity across both early and later stages of retrieval. Lastly, I anticipated atypical visual perspectives to be associated with increased functional recruitment and/or connectivity of brain regions underlying the manipulation of mental images in memory (e.g. precuneus) during autobiographical memory construction, due to increased demands on spatial transformation processes.

2.3 Methods

2.3.1. Participants

Participants included 25 healthy, right-handed young adults (age range: 18 to 30 years) with no prior history of neurological or psychiatric impairment, and who were not currently taking medication that affected mood or cognitive function. Participants provided informed written consent as approved by the School of Psychology at the University of Sussex. Five participants were excluded from the analysis due to issues during the fMRI session (i.e. movement greater than 3 mm, $n = 3$; not following instructions, $n = 1$; and technical issues during data collection, $n = 1$). Thus, the final analysis was performed on 20 participants (8 women; mean age = 22.5 years, $SD = 2.89$).

2.3.2 Procedure

The study involved two separate sessions. In a pre-scanning session, participants were asked to provide titles for 130 distinct and sufficiently specific spatial locations they had visited in the last three years (e.g., *arcade of the Brighton Pier* versus *Brighton Pier*). Each location was rated according to familiarity, vividness, and emotional intensity on 7-point scales from 1 = low to 7 = high, as well as the date of the last visit (1 = > 2 years, 2 = last 2 years, 3 = last year, 4 = last 6 months, 5 = last month, 6 = last week, 7 = today). The spatial locations were then randomly assigned to one of six experimental conditions (described below) and matched across the subjective ratings. Thus, there were no initial differences in the nature of the spatial location cues within each condition (see Table 1 in Appendix A).

The fMRI scanning session took place five to nine days later (mean in days = 6.63, $SD = .96$). On each trial, participants were presented with a spatial location cue and asked either to retrieve a specific autobiographical memory that had occurred at that location (i.e., autobiographical memory task) or to mentally visualize the spatial location without retrieving a specific autobiographical memory (i.e., control task). To distinguish between construction and elaboration phases, participants were asked to press a button once they had thought of a specific autobiographical memory or could visualize the spatial location, and then to continue to elaborate upon the memory or spatial visualization in as much detail as possible (e.g., Daselaar et al., 2008; McCormick et al., 2015; St. Jacques et al., 2011). Participants were given 17.5 s for the entire retrieval or visualization period.

To investigate the influence of visual perspective on construction and elaboration phases of autobiographical memory retrieval, we asked participants to adopt OE or OB perspectives. We also manipulated the typicality of the visual perspective in order to better understand how adopting multiple visual perspectives influences autobiographical memory retrieval (e.g., Rice & Rubin, 2011). In the OE perspective conditions, participants were asked to retrieve autobiographical memories as if they were seeing the event from a location centred within their body, either from a typical OE vantage point (OE Same) or from an atypical OE vantage point in which they mentally rotated the scene by switching left and right (OE Reverse). In the OB conditions, participants were asked to retrieve autobiographical memories as if seeing themselves in the event, outside of their body at a distance within six feet, either from a typical OB vantage point at eye

level (OB Eye Level) or from an atypical OB vantage point at floor level (OB Floor Level). In the control task, participants were also asked to visualize the spatial location from a typical vantage point that included the proximal aspects of the location (e.g., zooming in on the location within the Brighton Pier; Spatial Near), or from an atypical vantage point that included the distal aspects of the location (e.g., zooming out on the location of the Brighton Pier in relation to the city of Brighton; Spatial Far).

Immediately following each trial, participants were asked to provide subjective ratings of vividness, emotional intensity, and perspective maintenance (i.e. the ease with which the specified perspective was sustained), each on 4-point scales from 1 = low to 4 = high. Participants had 2.5 s for each rating and responded using a four button MRI-compatible response box. Prior to scanning, participants conducted a practice session to familiarize them with the study conditions and timings of the responses.

There were six functional runs consisting of either 18 trials (four runs) or 24 trials (two runs), for a total of 20 trials per condition. Trial order was pseudo-randomized, such that no condition was repeated more than twice consecutively. Trials were separated by an active baseline consisting of a left versus right decision task, which was equally spaced across a variable length (2.5 to 10 s; e.g., Stark & Squire, 2001) and distributed exponentially such that shorter inter-trial intervals occurred more frequently than longer.

2.3.3. MRI Data Acquisition and Preprocessing

Functional and structural images were collected on a 1.5 Siemens MRI scanner. Detailed anatomical data were collected using a multi-planar rapidly acquired gradient echo (MPRAGE) sequence. Functional images were acquired using a T2*-weighted echo planar sequence (TR = 2500ms, TE = 43ms, FOV = 192 mm x 192 mm, Slice Thickness = 3mm). Whole-brain coverage was obtained via 33 coronal oblique slices, acquired at an angle corresponding to AC-PC alignment in an ascending fashion, with a 3 x 3 mm in-plane resolution.

Preprocessing of functional images was performed using SPM12 (Wellcome Department of Imaging Neuroscience, London, UK) using standard methods. Functional images were corrected for differences in acquisition time between slices for each whole brain volume using slice-timing, realigned within and across runs to correct for head movement, spatially normalized to the Montreal Neurological Institute (MNI) template (resampled at 2 x 2 x 2 mm voxels), and then spatially smoothed using a Gaussian kernel (8 mm full-width at half maximum).

2.3.4 Behavioral Data Analysis

We conducted 3 (Condition: OE, OB, spatial) x 2 (Visual Perspective: typical, atypical) repeated measures ANOVAs on reaction time to construct the event and in scan subjective ratings (separately for vividness, emotional intensity, and perspective maintenance). Post-hoc comparisons were Bonferroni corrected and appropriate tests were applied when assumptions of sphericity were violated. One participant was excluded from the behavioral analyses of the subjective ratings due to an insufficient number of responses.

2.3.5 fMRI Analysis: Partial Least Squares

To analyze the fMRI data, we used spatiotemporal task PLS, a multivariate analysis approach that determines the optimal least squares fit between task conditions and distributed brain activity during experimental trials (Lin et al., 2003; McIntosh & Lobaugh 2004). The advantage of using PLS in the current study is that it characterizes changes in task-related brain activity at multiple time lags across the length of the experimental trial. Here, we specified a 17.5 s temporal window (i.e., 7 time lags, each equal to 2.5 s or 1 TR), to examine the multivariate pattern of brain activity during the retrieval or visualization period.

A cross-covariance matrix was created for each trial, including all participants and conditions, based on a design matrix containing condition information and a data matrix containing brain voxels. Singular value decomposition was applied to the cross-covariance matrix resulting in a set of extracted orthogonal components or latent variables (LVs) that provide the best fit of the data. Each LV reflects a set of contrasts that characterize the differences or similarities among the task conditions, and an associated pattern of distributed brain activity by time lag. LVs are associated with singular values, or the proportion that each LV contributes to the overall covariance between task conditions and brain activation. Each voxel is linked to a salience score, dependent on the observed covariances. Each salience can then be multiplied by the blood oxygen level dependent (BOLD) signal value of its associated voxel and summed across all voxels to yield a brain score, which can then be used to compare patterns of brain activity across the task conditions. Greater activity in brain regions with

positive saliences on a LV will produce positive mean brain scores for a given condition over each time point, while negative saliences will produce negative mean brain scores. LVs are progressively extracted in successively smaller amounts until all the data are accounted for.

The statistical significance of the LVs was determined using 500 permutation tests (e.g., Addis et al., 2004; Burianova et al., 2010), which applies singular value decomposition to calculate a new set of LVs after randomly re-ordering the data matrix rows. The newly obtained singular value of each LV is then compared to the originally derived value to create an updated weighted probability of the original singular value, dependent on the number of times it is exceeded by the results of each permutation test (McIntosh et al., 1996). The reliability of the results was assessed by 300 bootstrap estimations on the standard error of the saliences for the voxels within each LV (e.g., Addis, Pan, Vu, Laiser, & Schacter, 2009; Addis et al., 2004), which involves randomly re-sampling participants with replacement. Clusters larger than 20 contiguous voxels with a bootstrap ratio greater than three are reported (approximate $p = .001$). Peaks within each cluster were specified based on the voxel with the highest bootstrap ratio in a 1 cm cube centred on the voxel. Given that PLS analysis identifies patterns of activity across the whole brain in a single step, corrections for multiple comparisons are not required.

We employed three types of PLS analysis in the current study. First, we took a data driven, mean-centered approach in the form of a spatiotemporal task PLS analysis to examine the maximal differences between the six study conditions.

Second, we conducted separate mean-centred behavioral PLS analyses to identify patterns of brain activity associated with the in-scan subjective ratings of vividness, emotional intensity, and perspective maintenance, as well as the reaction time to construct an autobiographical memory or visualize the spatial location. For each behavioral PLS analysis, a cross-covariance matrix was computed across each trial including all participants and tasks by comparing a design matrix containing all voxels with a matrix containing the behavioral data in question.¹ Third, we employed a mean-centered seed PLS analyses to examine how visual perspective influenced the functional connectivity with the hippocampus over the time course of AM retrieval. We identified a seed region within the left anterior portion of hippocampus (MNI: $x = -26$, $y = -6$, $z = -22$), from the spatiotemporal task PLS analysis in time lag 6 (i.e. 15s after cue onset), that was sensitive to changes in visual perspective during AM retrieval. The average BOLD values in the hippocampal seed region along with its two nearest neighboring voxels for each participant at each time lag was then extracted and compared with activity in all other brain voxels separately within each condition. The same temporal window (i.e. 2.5 seconds corresponding to one TR) was applied for each PLS analysis.

2.4 Results

2.4.1 Behavioral Results

In general, we found that participants were slower to construct autobiographical memories than to visualize spatial locations, especially when

¹ Data from one participant was excluded in the behavioral PLS analyses on subjective ratings, due to an insufficient number of behavioral responses.

adopting an atypical OE perspective (for *means* and *SDs* see Table 1). There was a significant main effect of condition on the reaction time to construct an autobiographical memory compared to visualizing a spatial location, $F(2, 38) = 9.00$, $p = .001$, $\eta_p^2 = .32$, reflecting slower reaction times in the OE ($M = 4.30$, $SD = 1.65$) and OB ($M = 4.28$, $SD = 1.61$) conditions compared to the spatial visualization condition ($M = 3.75$, $SD = 1.24$), p 's $< .05$. The main effect was qualified by an interaction between condition and typicality, $F(2, 36) = 8.75$, $p = .001$, $\eta_p^2 = .31$. Follow-up tests indicated that the reaction time to construct events was slower in the atypical versus typical OE conditions, $p = .01$. For typical visual perspectives, reaction time was also slower in the OB compared to both the OE and spatial conditions, p 's $< .01$, whereas for atypical visual perspectives, reaction time was slower for the OE compared to the spatial condition, $p = .004$.

Table 1. Behavioural Ratings and Reaction Time

| | Autobiographical Memory Retrieval | | | | Control Task | |
|--------------------------------|-----------------------------------|-------------|-------------|-------------|-----------------------|-------------|
| | Own Eyes | | Observer | | Spatial Visualization | |
| | Typical | Atypical | Typical | Atypical | Typical | Atypical |
| Construction RT (s) | 4.09 (1.67) | 4.51 (1.69) | 4.40 (1.69) | 4.16 (1.58) | 3.68 (1.34) | 3.82 (1.18) |
| Vividness | | | | | | |
| Response | 3.18 (.39) | 2.71 (.47) | 2.90 (.51) | 2.76 (.55) | 2.97 (.51) | 2.74 (.57) |
| RT (s) | .93 (.23) | 1.01 (.23) | .96 (.28) | 1.00 (.26) | .91 (.26) | .96 (.32) |
| Emotional Intensity | | | | | | |
| Response | 2.56 (.45) | 2.33 (.53) | 2.39 (.48) | 2.32 (.53) | 2.15 (.48) | 2.11 (.58) |
| RT (s) | .96 (.29) | .96 (.34) | 1.01 (.32) | .97 (.30) | .89 (.40) | .96 (.33) |
| Perspective Maintenance | | | | | | |
| Response | 2.90 (.64) | 2.44 (.51) | 2.73 (.65) | 2.57 (.60) | 2.80 (.71) | 2.68 (.57) |
| RT (s) | 1.26 (.29) | 1.28 (.26) | 1.28 (.27) | 1.32 (.29) | 1.25 (.28) | 1.26 (.25) |

Mean (Standard Deviation)

Turning to the in-scan subjective ratings, we found that typical versus atypical visual perspectives generally received higher subjective ratings (for *means*

and SDs see Table 1). First, for vividness ratings there was a main effect of typicality, $F(1, 18) = 32.34, p < .001, \eta_p^2 = .64$, reflecting higher ratings for typical ($M = 3.02, SD = .48$) relative to atypical perspectives ($M = 2.74, SD = .52$). The main effect of typicality was qualified by an interaction with condition, $F(2, 36) = 4.21, p = .02, \eta_p^2 = .19$ (see Figure 1). Follow-up tests indicated that vividness ratings were higher for typical compared to atypical perspectives in the OE and spatial conditions, p 's $< .05$, but there was only a marginal effect in the OB condition, $p = .06$. Additionally, for typical perspectives, vividness ratings were higher in the OE compared to both the OB and spatial conditions. However, there were no differences in vividness ratings between the conditions within atypical perspectives.

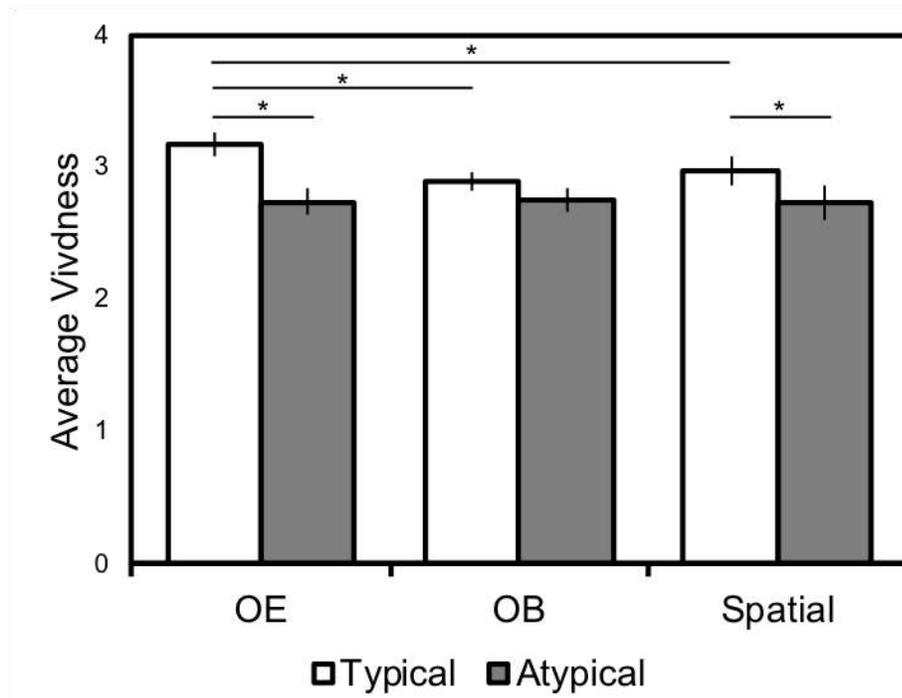


Figure 1. In-Scan Vividness Ratings. Typical perspectives were associated with higher vividness than atypical perspectives in the OE and spatial visualization conditions. Among typical perspectives, the OE condition involved greater vividness compared to OB and spatial visualization conditions.

Second, for emotional intensity ratings there was a main effect of typicality, $F(1, 18) = 6.79, p = .02, \eta_p^2 = .27$, with higher ratings for typical ($M = 2.37, SD = .49$) than atypical ($M = 2.25, SD = .55$) perspectives. There was also a main effect of condition, $F(2, 36) = 15.82, p < .001, \eta_p^2 = .47$, reflecting higher ratings in the OE ($M = 2.44, SD = .49$) and OB ($M = 2.35, SD = .49$) conditions compared to the spatial conditions ($M = 2.13, SD = .52$), p 's $< .005$.

Third, for perspective maintenance ratings there was a main effect of typicality, $F(1, 18) = 7.32, p = .01, \eta_p^2 = .29$, reflecting higher ratings for typical ($M = 2.81, SD = .66$) versus atypical ($M = 2.56, SD = .56$) perspectives. However, the main effect of typicality was qualified by an interaction with condition, $F(2, 36) = 6.28, p = .005, \eta_p^2 = .26$ (see Figure 2). Follow-up tests indicated higher perspective maintenance ratings in the typical versus atypical OE conditions, $p = .004$. Within typical perspectives, there were higher perspective maintenance ratings for OE compared to OB conditions, $p = .03$, whereas within atypical perspectives there were marginally lower ratings for OE than spatial conditions, $p = .05$.

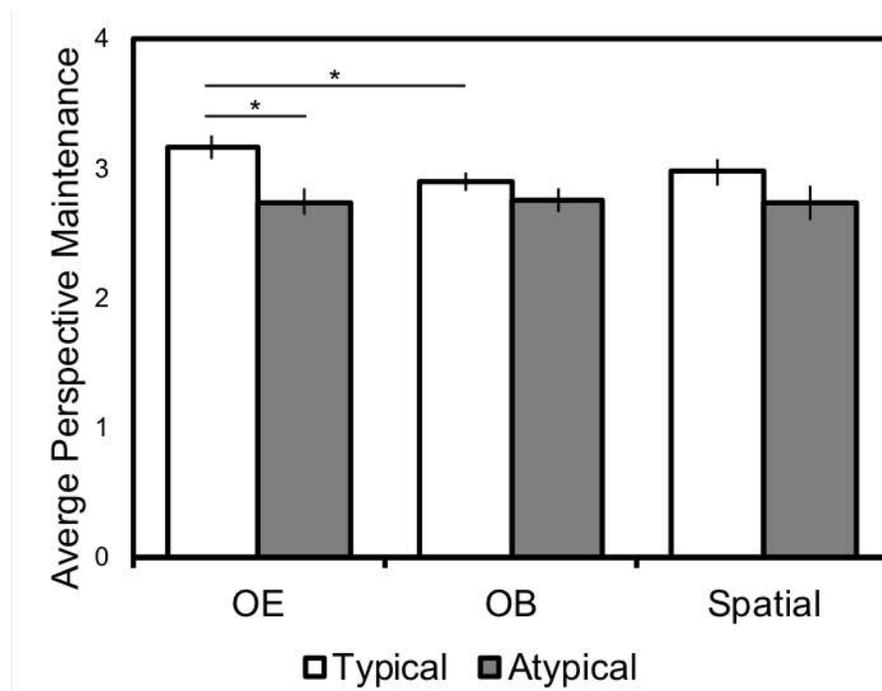


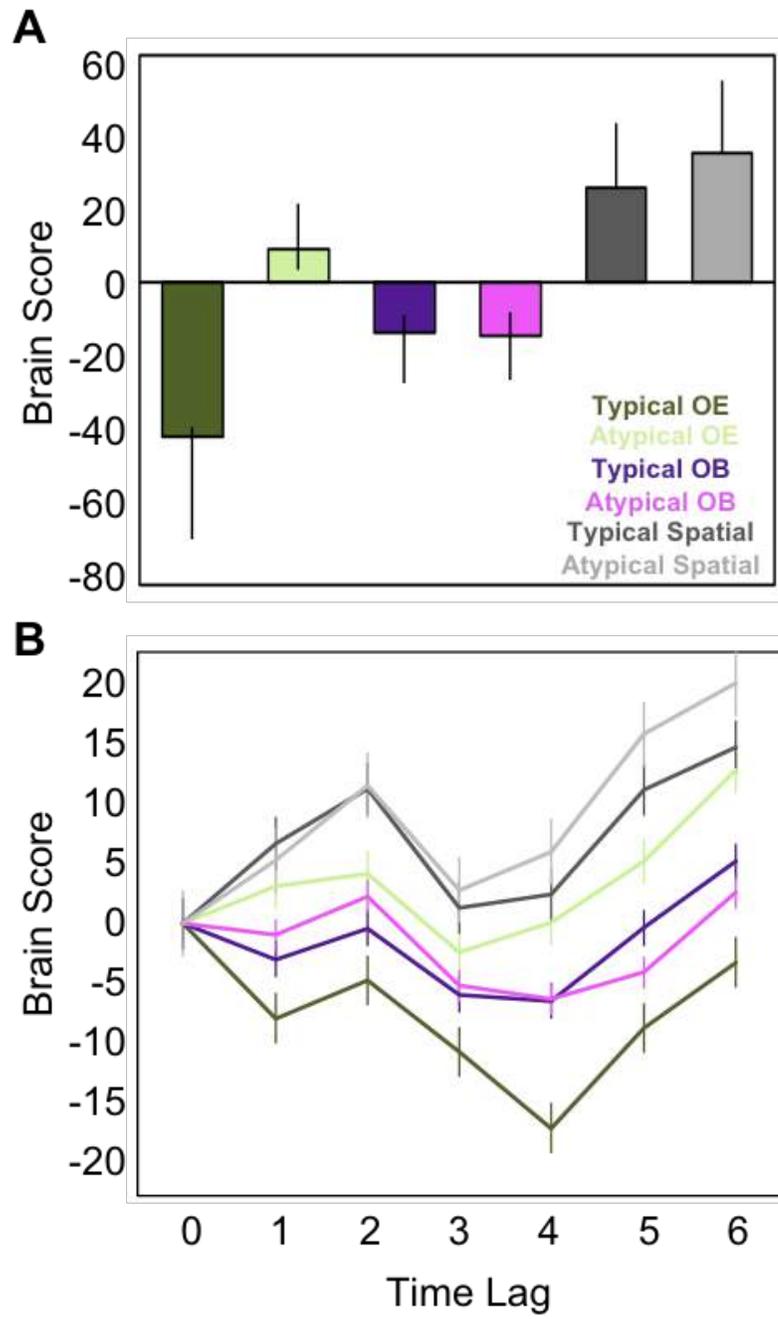
Figure 2. In-Scan Perspective Maintenance Ratings. Typical OE perspectives were associated with higher perspective maintenance compared to atypical OE and typical OB perspectives.

In sum, the behavioral findings suggest that the typicality of the perspective influenced the construction and in-scan ratings in both the autobiographical memory and control tasks. In particular, AMs retrieved from typical OE perspectives were faster to construct compared to atypical OE perspectives, associated with greater vividness compared to both typical OB and spatial conditions, and higher perspective maintenance compared to typical OB perspectives. As expected, emotional intensity was higher when retrieving autobiographical memories than when visualizing a spatial location.

2.4.2 Spatiotemporal Task PLS

The main goal of the study was to examine how visual perspective influences the construction and elaboration of autobiographical memory retrieval.

The spatiotemporal task PLS analysis identified one significant LV, which accounted for 29.10% of the variance ($p < .0001$; see Figure 3A and Table 2). This LV maximally dissociated the typical OE and both OB conditions (negative brain scores) from the spatial and atypical OE conditions (positive brain scores). A 3 (Task: AM retrieval from an own eyes perspective, AM retrieval from an observer perspective, spatial visualization) x 2 (Typicality: typical, atypical) repeated measures ANOVA on the brain scores revealed main effects of both task, $F(2,38) = 32.60$, $p < .001$, $\eta_p^2 = .63$, and typicality, $F(2,38) = 26.92$, $p < .001$, $\eta_p^2 = .59$, which were qualified by an interaction, $F(2,38) = 12.21$, $p < .001$, $\eta_p^2 = .39$. Follow-up paired t-tests adjusted for multiple comparisons using Bonferroni corrections revealed that the typical OE condition was assigned a greater negative brain score compared to both the typical ($p = .01$) and atypical ($p = .004$) OB condition, suggesting that the former contributed more to the overall pattern identified by the LV. Similarly, within the positive saliences there was less loading on the atypical OE than the atypical ($p = .008$), but not typical ($p = .03$), spatial control tasks.



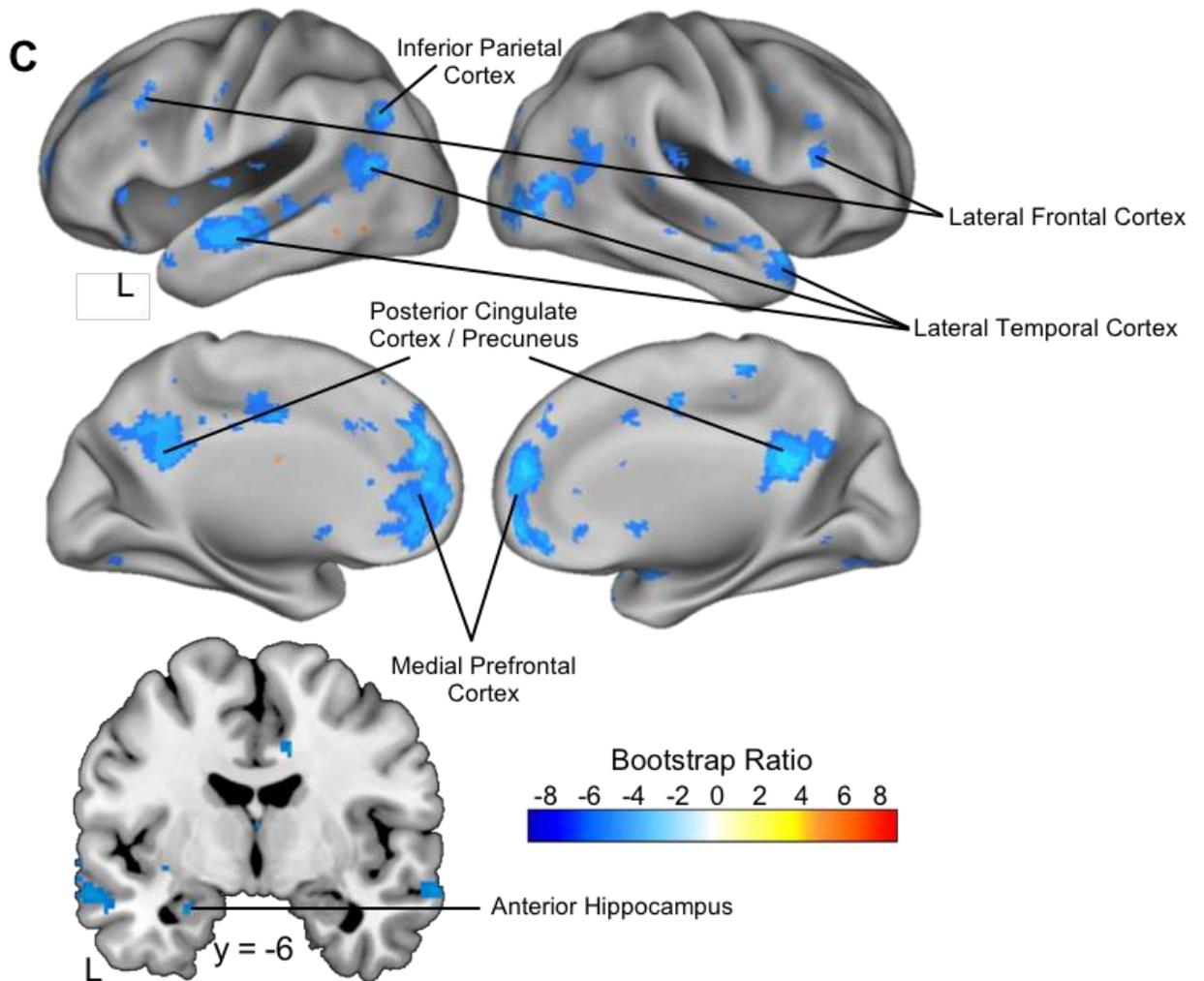


Figure 3. Spatiotemporal Task PLS Results. (A) The weighted average activation per condition across all voxels in all participants across the length of the retrieval period for the significant LV extracted from the spatiotemporal task PLS. Error bars represent the 95% confidence interval and are based on bootstrap estimates. Positive brain scores are associated with spatial visualization and AM retrieval from an atypical OE perspective. Negative brain scores are associated with AM retrieval from typical OE and both OB perspectives. (B) The average brain score for each condition across each time lag within the trial. Each time lag corresponds to 2.5s (i.e., one TR). (C) Activation patterns corresponding to the positive and negative brain scores in time lag 6. All images depict a BSR threshold of ± 3 .

Table 2. Spatiotemporal Task PLS

| Region | BA | MNI Coordinates | | | Ratio | Cluster Size | | | | | | | | | | |
|---------------------------------|----|-----------------|-----|-------|-------|--------------|--|--|--|--|--|--|--|--|--|--|
| | | x | y | z | | | | | | | | | | | | |
| Time Lag 1 | | | | | | | | | | | | | | | | |
| Positive Saliences | | | | | | | | | | | | | | | | |
| Lateral Frontopolar Cortex | 10 | -44 | 38 | 20 | 4.32 | 69 | | | | | | | | | | |
| Ventrolateral PFC | 47 | 44 | 24 | -14 | 4.05 | 21 | | | | | | | | | | |
| Supplementary Motor Area | 6 | -8 | -16 | 48 | 3.90 | 21 | | | | | | | | | | |
| Premotor Cortex | 6 | 38 | 4 | 56 | 5.09 | 28 | | | | | | | | | | |
| Motor Cortex | 4 | 38 | -20 | 60 | 3.89 | 22 | | | | | | | | | | |
| Auditory Cortex | 41 | -40 | -24 | 10 | 7.36 | 225 | | | | | | | | | | |
| Insula | 13 | -30 | 20 | -8 | 4.76 | 109 | | | | | | | | | | |
| Anterior Temporal Cortex | 38 | 40 | 6 | -20 | 4.54 | 156 | | | | | | | | | | |
| Middle Temporal Cortex | 22 | 52 | -14 | -12 | 5.43 | 82 | | | | | | | | | | |
| | 21 | 50 | -38 | 2 | 4.99 | 34 | | | | | | | | | | |
| Somatosensory Cortex | 1 | 48 | -12 | 14 | 4.65 | 151 | | | | | | | | | | |
| | 1 | -64 | -14 | 14 | 4.39 | 94 | | | | | | | | | | |
| | 5 | -2 | -40 | 68 | 4.97 | 83 | | | | | | | | | | |
| | 1 | -60 | -18 | 34 | 4.58 | 48 | | | | | | | | | | |
| Superior Parietal Cortex | 7 | -26 | -56 | 64 | 4.61 | 99 | | | | | | | | | | |
| | 7 | 30 | -60 | 56 | 4.01 | 49 | | | | | | | | | | |
| Inferior Parietal Cortex | 40 | -44 | -48 | 46 | 4.65 | 203 | | | | | | | | | | |
| | 40 | 44 | -32 | 46 | 4.11 | 66 | | | | | | | | | | |
| | 40 | -52 | -40 | 34 | 4.01 | 39 | | | | | | | | | | |
| Fusiform Cortex | 37 | 42 | -58 | -14 | 5.45 | 178 | | | | | | | | | | |
| Crus I Lobule of the Cerebellum | 28 | -72 | -28 | 4.35 | 20 | | | | | | | | | | | |
| Cerebellum Lobule IV, V | 18 | -36 | -26 | 4.08 | 31 | | | | | | | | | | | |
| Time Lag 2 | | | | | | | | | | | | | | | | |
| Positive Saliences | | | | | | | | | | | | | | | | |
| Ventrolateral PFC | 44 | 58 | 16 | 10 | 4.13 | 39 | | | | | | | | | | |
| Premotor Cortex | 6 | 18 | -6 | 60 | 4.58 | 26 | | | | | | | | | | |
| Motor Cortex | 4 | -40 | -20 | 54 | 4.30 | 87 | | | | | | | | | | |
| Auditory Cortex | 41 | -44 | -20 | 8 | 4.04 | 40 | | | | | | | | | | |
| Insula | 13 | -30 | 18 | -14 | 4.00 | 58 | | | | | | | | | | |
| | 13 | 30 | 22 | 10 | 4.00 | 34 | | | | | | | | | | |
| Anterior Temporal Cortex | 38 | 46 | 4 | -12 | 5.27 | 172 | | | | | | | | | | |
| | 38 | -42 | 4 | -16 | 4.25 | 55 | | | | | | | | | | |
| Anterior Parahippocampal Gyurs | | 24 | 10 | -24 | 4.35 | 37 | | | | | | | | | | |
| Somatosensory Cortex | 1 | 46 | -12 | 14 | 4.43 | 26 | | | | | | | | | | |
| Superior Parietal Cortex | 7 | -30 | -48 | 54 | 3.84 | 27 | | | | | | | | | | |
| Fusiform Cortex | 37 | 42 | -56 | -12 | 4.16 | 49 | | | | | | | | | | |
| Visual Cortex | 19 | -38 | -68 | 6 | 4.54 | 38 | | | | | | | | | | |
| Cerebellum Lobule VI | 18 | -68 | -20 | 4.93 | 104 | | | | | | | | | | | |
| Time Lag 3 | | | | | | | | | | | | | | | | |
| Positive Saliences | | | | | | | | | | | | | | | | |
| Premotor Cortex | 6 | 14 | 22 | 56 | 3.97 | 20 | | | | | | | | | | |
| Anterior Temporal Cortex | 38 | 40 | 8 | -20 | 4.25 | 70 | | | | | | | | | | |
| Inferior Parietal Cortex | 40 | -56 | -28 | 46 | 4.17 | 29 | | | | | | | | | | |
| Fusiform Cortex | 37 | 36 | -42 | -10 | 4.33 | 35 | | | | | | | | | | |
| Negative correlations | | | | | | | | | | | | | | | | |
| Dorsomedial PFC | 10 | -12 | 60 | 6 | -5.19 | 48 | | | | | | | | | | |
| | 10 | -8 | 50 | 18 | -4.10 | 23 | | | | | | | | | | |
| Dorsolateral PFC | 9 | -14 | 26 | 42 | -4.06 | 21 | | | | | | | | | | |
| | 9 | 62 | 26 | 14 | -3.92 | 20 | | | | | | | | | | |
| Ventrolateral PFC | 45 | -56 | 22 | 20 | -4.34 | 127 | | | | | | | | | | |
| | 47 | -42 | 24 | -8 | -3.85 | 55 | | | | | | | | | | |
| | 44 | 40 | 18 | 18 | -3.67 | 44 | | | | | | | | | | |
| | 45 | -40 | 30 | 6 | -4.18 | 34 | | | | | | | | | | |
| Superior Temporal Cortex | 22 | -66 | -46 | 14 | -4.91 | 61 | | | | | | | | | | |
| | 22 | -50 | -20 | -6 | -4.22 | 39 | | | | | | | | | | |
| Somatosensory Cortex | 1 | 52 | -10 | 26 | -3.86 | 18 | | | | | | | | | | |
| Inferior Parietal Cortex | 39 | -52 | -66 | 18 | -4.55 | 124 | | | | | | | | | | |
| | 40 | 40 | -28 | 20 | -3.84 | 32 | | | | | | | | | | |
| Visual Cortex | 19 | -42 | -86 | 12 | -3.84 | 57 | | | | | | | | | | |
| | 18 | 34 | -82 | 6 | -3.69 | 35 | | | | | | | | | | |
| | 18 | 22 | -98 | 16 | -3.74 | 21 | | | | | | | | | | |
| Time Lag 4 | | | | | | | | | | | | | | | | |
| Positive Saliences | | | | | | | | | | | | | | | | |
| Fusiform Cortex | 37 | 36 | -42 | -10 | 4.33 | 35 | | | | | | | | | | |
| Cerebellum Lobule IV, V | 18 | -32 | -22 | 4.04 | 40 | | | | | | | | | | | |
| Negative Saliences | | | | | | | | | | | | | | | | |
| Orbitofrontal Cortex | 47 | -24 | 10 | -22 | -4.69 | 39 | | | | | | | | | | |
| Ventromedial PFC | 11 | 4 | 32 | -14 | -5.19 | 132 | | | | | | | | | | |
| Dorsolateral PFC | 10 | -16 | 50 | 8 | -5.60 | 1361 | | | | | | | | | | |
| | 8 | 28 | 32 | 54 | -5.27 | 85 | | | | | | | | | | |
| Ventrolateral PFC | 47 | -40 | 20 | -10 | -5.14 | 361 | | | | | | | | | | |
| | 47 | 54 | 32 | -6 | -4.60 | 79 | | | | | | | | | | |
| | 47 | 40 | 32 | -6 | -5.20 | 66 | | | | | | | | | | |
| | 44 | -38 | 20 | 18 | -4.51 | 54 | | | | | | | | | | |
| | 44 | -38 | 20 | 18 | -4.51 | 54 | | | | | | | | | | |
| Anterior Premotor Cortex | 8 | 28 | 32 | 54 | -5.27 | 85 | | | | | | | | | | |
| Premotor Cortex | 6 | 42 | 2 | 60 | -4.42 | 28 | | | | | | | | | | |
| Auditory Cortex | 41 | 40 | -82 | -8 | -3.66 | 74 | | | | | | | | | | |
| Superior Temporal Cortex | 22 | 42 | -18 | -4 | -3.91 | 49 | | | | | | | | | | |
| Middle Temporal Cortex | 21 | 64 | -2 | -18 | -6.74 | 368 | | | | | | | | | | |
| | 21 | -52 | -26 | -8 | -5.50 | 314 | | | | | | | | | | |
| Posterior Cingulate Cortex | 23 | 4 | -50 | 24 | -8.23 | 574 | | | | | | | | | | |
| Inferior Parietal Cortex | 39 | -54 | -64 | 18 | -4.69 | 309 | | | | | | | | | | |
| Visual Cortex | 19 | -32 | -66 | -14 | -5.73 | 100 | | | | | | | | | | |
| | 19 | -22 | -84 | 16 | -3.95 | 27 | | | | | | | | | | |
| | 18 | -22 | -88 | -12 | -3.92 | 56 | | | | | | | | | | |
| Caudate | | -6 | 14 | -10 | -5.74 | 304 | | | | | | | | | | |
| Cerebellum Lobule VI, V | | -4 | -40 | -6 | -4.78 | 42 | | | | | | | | | | |
| Time Lag 5 | | | | | | | | | | | | | | | | |
| Negative Saliences | | | | | | | | | | | | | | | | |
| Lateral Frontopolar Cortex | 10 | -26 | 40 | 22 | -4.48 | 327 | | | | | | | | | | |
| Dorsolateral PFC | 46 | 56 | 34 | 18 | -4.25 | 154 | | | | | | | | | | |
| | 46 | -52 | 28 | 20 | -3.94 | 40 | | | | | | | | | | |
| Ventrolateral PFC | 47 | -42 | 24 | -18 | -4.41 | 246 | | | | | | | | | | |
| | 45 | -32 | 30 | 2 | -4.96 | 194 | | | | | | | | | | |
| | 47 | 24 | 28 | -14 | -4.57 | 89 | | | | | | | | | | |
| Anterior Premotor Cortex | 8 | -46 | 20 | 32 | -4.22 | 72 | | | | | | | | | | |
| Premotor Cortex | 6 | -48 | -8 | 42 | -3.77 | 33 | | | | | | | | | | |
| Motor Cortex | 4 | 8 | -34 | 64 | -5.63 | 70 | | | | | | | | | | |
| | 4 | 60 | -2 | 10 | -4.00 | 49 | | | | | | | | | | |
| | 4 | -26 | -26 | 66 | -3.86 | 32 | | | | | | | | | | |
| Amygdala | 32 | 6 | -20 | -4.47 | 68 | | | | | | | | | | | |
| Auditory Cortex | 4 | -60 | -6 | 4 | -3.75 | 24 | | | | | | | | | | |
| Superior Temporal Cortex | 38 | 50 | 16 | -26 | -5.32 | 394 | | | | | | | | | | |
| | 22 | 50 | -14 | -8 | -4.26 | 120 | | | | | | | | | | |
| Middle Temporal Cortex | 21 | -60 | -10 | -16 | -7.49 | 983 | | | | | | | | | | |
| | 22 | 58 | -38 | 6 | -3.73 | 33 | | | | | | | | | | |
| Anterior Cingulate Cortex | 32 | -2 | 46 | 2 | -7.91 | 3334 | | | | | | | | | | |
| | 24 | -4 | -10 | 44 | -4.84 | 312 | | | | | | | | | | |
| | 25 | -2 | 12 | -8 | -4.16 | 60 | | | | | | | | | | |
| Posterior Cingulate Cortex | 23 | 6 | -50 | 24 | -8.65 | 1281 | | | | | | | | | | |
| | 23 | -8 | -32 | 36 | -4.69 | 76 | | | | | | | | | | |
| Inferior Parietal Cortex | 39 | -44 | -68 | 36 | -4.92 | 731 | | | | | | | | | | |

Critically, the PLS approach also allowed investigation of how the LV differed across each time lag spanning construction and elaboration phases. The timing of the multivariate pattern associated with the positive and negative saliences differed (see Figure 3B and Figure 1 in Appendix A). Neural recruitment associated with the spatial and atypical OE conditions emerged earlier, demonstrating an initial peak at time lag 2 (i.e., 5 s following cue onset). In contrast, neural recruitment associated with the typical OE and both OB conditions emerged later, peaking in response during time lag 4 (i.e., 9 s following cue onset). Given that the average length of construction was 4.11 s ($SD = 1.46$ s), these findings show that visual perspective is connected with the neural mechanisms that support later elaboration of autobiographical memories.

The spatial and atypical OE conditions recruited frontoparietal and lateral temporal cortices, which may reflect additional control processes required in these tasks (Dosenbach et al., 2007; Seeley et al., 2007; Vincent et al., 2008), relying on the retrieval of semantic information related to the autobiographical memory or familiar location (Binder & Desai, 2011; Maguire, 2000; Svoboda et al., 2006; see Figure 3C and Table 2). In contrast, autobiographical memories retrieved in the typical OE and both OB conditions recruited anterior and posterior midline, MTL (including left anterior hippocampus and right amygdala), ventrolateral PFC, lateral temporal and inferior posterior parietal cortices (see Figure 3C and Table 2), which overlap with regions frequently recruited during autobiographical memory retrieval (e.g., Andrews-Hanna et al. 2015; Svoboda et al. 2006; Cabeza & St. Jacques 2007). However, the pattern of neural recruitment contributed more to the typical

OE condition compared to the OB conditions, demonstrating that these core autobiographical memory regions are less engaged when retrieving memories from OB perspectives.

2.4.3. Behavioral PLS.

I conducted additional behavioral PLS analyses to determine whether the differences in the multivariate pattern during construction and elaboration overlapped with the pattern of neural activity sensitive to the reaction time to construct a memory or behavioral ratings. Separate behavioral PLS analyses were conducted on the reaction time to construct a memory or visualize the spatial location, as well as subjective ratings of perspective maintenance, vividness, and emotional intensity. These behavioral PLS analyses revealed brain regions positively and negatively correlated with construction reaction times and subjective ratings across conditions. In these analyses, positive correlations corresponded to shorter retrieval times and lower subjective ratings, whereas negative correlations corresponded to longer retrieval times and higher online subjective ratings. Overall, these additional behavioral PLS analyses revealed that there was limited neural overlap with effects obtained from the spatiotemporal task PLS, suggesting that behavioral differences in construction reaction time, vividness, emotional intensity, and perspective maintenance do not fully account for the reported differences in visual perspective in the spatiotemporal task PLS analysis.

First, turning to reaction time, a single significant LV explained 45.37% of the variance equally across all conditions ($p = .001$; see Figure 4 and Table 3). Shorter reaction times (i.e., positive correlations) to construct an AM and visualize

a spatial location were associated with a widespread pattern of activation in bilateral frontal and temporal cortices, anterior cingulate cortex, and medial PFC. Notably, only the medial PFC overlapped with the pattern of regions that distinguished OE Same and OB Floor conditions in the spatiotemporal PLS (see Figure 5). Longer reaction times (i.e., negative correlations) were associated with neural recruitment including right precuneus and bilateral visual cortices, but there was no overlap with the spatiotemporal PLS results.

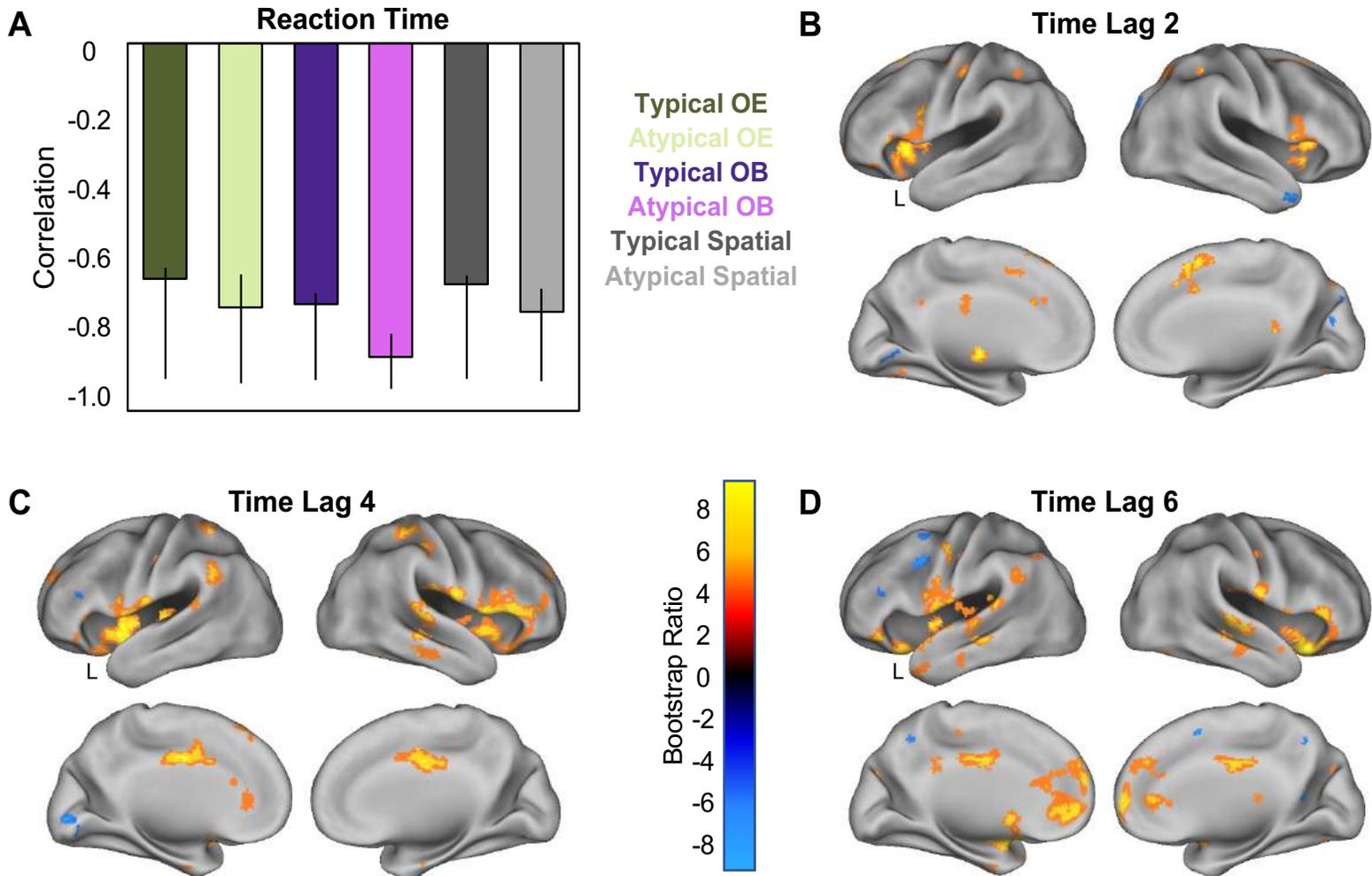


Figure 4. Reaction Time Behavioural PLS. (A) Correlation scores associated with the significant LV from the behavioural PLS on reaction times to construct an AM and visualize the spatial location. Error bars represent the 95% confidence interval, based on bootstrap estimates. Patterns of activation mapped onto the surface of the brain for time lags 2 (B), 4 (C), and 6 (D) are also shown. All images depict a BSR threshold of ± 3 .

Table 3. Behavioural PLS: Construction Time

| Region | BA | MNI Coordinates | | | Ratio | Cluster Size | Positive Correlations | Time Lag 4 | | | | | | |
|------------------------------|----|-----------------|-----|------|-------|--------------|------------------------------|------------|-----|-------|-------|-------|------|----|
| | | x | y | z | | | | | | | | | | |
| Positive Correlations | | | | | | | Dorsomedial PFC | 10 | -10 | 58 | 28 | 4.31 | 314 | |
| Time Lag 1 | | | | | | | 8 | -12 | 28 | 56 | 5.81 | 189 | | |
| Lateral Frontopolar Cortex | 10 | -20 | 46 | 8 | 6.15 | 178 | Lateral Frontopolar Cortex | 10 | -30 | 46 | 0 | 6.01 | 103 | |
| | 10 | -26 | 62 | -6 | 5.04 | 129 | Dorsolateral PFC | 9 | 14 | 46 | 36 | 5.57 | 234 | |
| | 11 | 14 | 56 | -12 | 4.44 | 111 | 9 | -34 | 26 | 32 | 5.14 | 43 | | |
| | 11 | -14 | 62 | -14 | 3.55 | 40 | 24 | 0 | -10 | 40 | 7.02 | 857 | | |
| Dorsolateral PFC | 9 | -32 | 26 | 34 | 5.34 | 116 | 32 | -2 | 42 | 4 | 4.13 | 179 | | |
| Ventrolateral PFC | 44 | -52 | 6 | 24 | 4.17 | 25 | 24 | 4 | 18 | 20 | 5.11 | 109 | | |
| | 45 | -42 | 18 | 8 | 3.64 | 23 | 13 | -46 | 2 | -2 | 8.15 | 3518 | | |
| Supplementary Motor Area | 6 | -10 | -8 | 54 | 4.58 | 52 | 13 | 40 | -4 | -16 | 3.62 | 23 | | |
| | 6 | 2 | 12 | 58 | 3.86 | 46 | 22 | 50 | 8 | -8 | 11.01 | 2952 | | |
| Premotor Cortex | 6 | -38 | 0 | 34 | 4.94 | 71 | 21 | 72 | -8 | -6 | 7.69 | 1600 | | |
| | 6 | 28 | 2 | 58 | 4.09 | 43 | 21 | -56 | -26 | -14 | 4.06 | 54 | | |
| Motor Cortex | 4 | -36 | -18 | 56 | 5.39 | 287 | 21 | -70 | -32 | -2 | 3.97 | 22 | | |
| Middle Temporal Cortex | 21 | 52 | -24 | -16 | 6.69 | 30 | 1 | -38 | -20 | 36 | 5.51 | 185 | | |
| | 21 | 50 | -38 | -2 | 4.42 | 25 | 1 | 48 | -12 | 24 | 4.50 | 21 | | |
| Somatosensory Cortex | 1 | -42 | -20 | 12 | 4.46 | 25 | 7 | -28 | -50 | 58 | 5.54 | 204 | | |
| | 1 | -32 | -42 | 64 | 4.02 | 25 | 39 | 44 | -44 | 36 | 6.07 | 744 | | |
| Superior Parietal Cortex | 7 | 22 | -74 | 46 | 4.70 | 148 | 39 | 36 | -60 | 36 | 4.54 | 28 | | |
| | 7 | -24 | -54 | 44 | 4.82 | 51 | 37 | 66 | -52 | 2 | 4.95 | 50 | | |
| Inferior Parietal Cortex | 39 | -56 | -52 | 32 | 4.44 | 21 | 37 | 46 | -62 | -22 | 4.63 | 50 | | |
| Visual Cortex | 19 | 36 | -70 | 20 | 4.93 | 84 | 37 | 52 | -64 | 2 | 3.37 | 21 | | |
| | 17 | 0 | -88 | 8 | 4.78 | 31 | 19 | -24 | -74 | 20 | 3.77 | 24 | | |
| | 17 | 12 | -64 | 12 | 3.58 | 23 | Putamen | 19 | -16 | 4 | -12 | 3.85 | 61 | |
| Thalamus | | -12 | -14 | -4 | 4.53 | 36 | 16 | 8 | -8 | -8 | 3.69 | 34 | | |
| | | -2 | -6 | 14 | 3.55 | 25 | Cerebellum Lobule III | 4 | -46 | -22 | 4.39 | 28 | | |
| Cerebellum Lobule VI | 40 | -38 | -32 | 4.55 | 21 | | | | | | | | | |
| Negative Correlations | | | | | | | Dorsolateral PFC | 46 | -36 | 32 | 18 | -5.34 | 75 | |
| Dorsomedial PFC | 10 | 12 | 48 | 18 | -5.79 | 133 | Anterior Premotor Cortex | 8 | 22 | 22 | 40 | -3.66 | 21 | |
| Anterior Premotor Cortex | 8 | 14 | 38 | 42 | -4.07 | 26 | Premotor Cortex | 6 | 32 | 2 | 44 | -4.72 | 67 | |
| Motor Cortex | 1 | 30 | -22 | 52 | -3.99 | 20 | 6 | 20 | 10 | 48 | -4.29 | 28 | | |
| Hippocampus | | -36 | -22 | -14 | -5.32 | 73 | 37 | -34 | -48 | -20 | -5.32 | 53 | | |
| Insula | 13 | -36 | -4 | 18 | -4.96 | 100 | 37 | -38 | -58 | -6 | -3.71 | 24 | | |
| | 13 | 44 | -12 | 12 | -4.92 | 44 | 18 | -8 | -86 | -2 | -4.84 | 99 | | |
| Posterior Cingulate Cortex | 23 | -18 | -42 | 26 | -4.57 | 31 | | | | | | | | |
| Supramarginal Cortex | 40 | 40 | -26 | 22 | -5.48 | 93 | Time Lag 5 | | | | | | | |
| Visual Cortex | 19 | -36 | -62 | -2 | -4.68 | 29 | Dorsomedial PFC | 10 | -12 | 62 | 16 | 7.22 | 3022 | |
| Time Lag 2 | | | | | | | Ventromedial PFC | 11 | -16 | 48 | -16 | 3.74 | 45 | |
| Positive Correlations | | | | | | | Lateral Frontopolar Cortex | 10 | -30 | 60 | -8 | 5.18 | 53 | |
| Lateral Frontopolar Cortex | 10 | -30 | 62 | -2 | 4.65 | 176 | 10 | -28 | 46 | -2 | 3.71 | 22 | | |
| | 10 | -20 | 48 | 22 | 5.44 | 75 | Ventrolateral PFC | 47 | -38 | 22 | -22 | 7.48 | 3418 | |
| | 11 | -24 | 46 | -14 | 3.62 | 35 | 8 | 40 | 14 | 52 | 3.90 | 22 | | |
| Dorsolateral PFC | 9 | -34 | 28 | 32 | 5.66 | 83 | Perirhinal Cortex | 36 | -28 | -8 | -36 | 6.70 | 99 | |
| Ventrolateral PFC | 47 | -44 | 40 | -20 | 3.92 | 55 | 36 | 28 | -14 | -30 | 5.19 | 38 | | |
| Supplementary Motor Area | 6 | -12 | 22 | 62 | 6.78 | 1020 | Insula | 13 | 50 | 6 | -6 | 9.91 | 5289 | |
| Premotor Cortex | 6 | -34 | -4 | 66 | 5.42 | 384 | 20 | 46 | -4 | -36 | 4.13 | 27 | | |
| | 6 | 40 | 8 | 62 | 4.80 | 186 | Anterior Cingulate Cortex | 24 | -4 | -6 | 34 | 6.40 | 669 | |
| | 6 | 30 | -8 | 46 | 4.19 | 65 | Posterior Cingulate Cortex | 23 | 14 | -48 | 32 | 4.05 | 21 | |
| Anterior Cingulate Cortex | 32 | -8 | 24 | 26 | 4.17 | 52 | 1 | -36 | -20 | 36 | 6.81 | 341 | | |
| Posterior Cingulate Cortex | 31 | -6 | -54 | 32 | 3.66 | 20 | 1 | 36 | -36 | 64 | 3.90 | 123 | | |
| Retrosplenial Cortex | 30 | 4 | -42 | 14 | 4.17 | 66 | 1 | 42 | -18 | 34 | 5.03 | 96 | | |
| Insula | 13 | -38 | 16 | 0 | 8.70 | 1606 | Superior Parietal Cortex | 1 | 52 | -26 | 54 | 3.56 | 61 | |
| | 13 | 34 | 18 | 2 | 7.06 | 1111 | 7 | -20 | -46 | 50 | 4.18 | 26 | | |
| Superior Parietal Cortex | 7 | 22 | -62 | 54 | 4.69 | 159 | Inferior Parietal Cortex | 39 | -54 | -52 | 36 | 6.61 | 306 | |
| | 7 | 36 | -44 | 52 | 4.17 | 21 | 40 | -48 | -22 | 16 | 5.75 | 272 | | |
| Inferior Parietal Cortex | 39 | -54 | -52 | 32 | 4.19 | 63 | 39 | 54 | -60 | 42 | 3.84 | 58 | | |
| | 40 | -48 | -20 | 14 | 4.07 | 22 | 39 | -48 | -62 | 48 | 4.49 | 32 | | |
| Fusiform Cortex | 37 | -28 | -62 | -12 | 4.89 | 42 | 37 | 46 | -62 | -20 | 5.79 | 777 | | |
| Visual Cortex | 19 | 30 | -72 | -14 | 3.66 | 29 | Visual Cortex | 19 | -22 | -78 | 24 | 7.20 | 79 | |
| | 18 | 34 | -66 | 16 | 4.89 | 27 | 19 | -30 | -66 | -14 | 4.06 | 57 | | |
| | 18 | 36 | -74 | 2 | 4.36 | 22 | Caudate | 6 | 6 | -6 | 5.78 | 176 | | |
| Pallidum | | -16 | -4 | 6 | 3.74 | 35 | Negative Correlations | | | | | | | |
| Thalamus | | -10 | -12 | 0 | 7.22 | 79 | Dorsolateral PFC | 46 | -38 | 32 | 20 | -4.62 | 55 | |
| Pons | | -2 | -26 | -30 | 5.29 | 98 | 9 | -26 | 30 | 34 | -3.88 | 31 | | |
| Cerebellum Lobule IV, V | 8 | -52 | -8 | 5.23 | 134 | 8 | 36 | 4 | 44 | -5.51 | 103 | | | |
| Negative Correlations | | | | | | | Supplementary Motor Area | 6 | 4 | 10 | 52 | -4.88 | 51 | |
| Superior Temporal Cortex | 38 | 44 | 16 | -34 | -4.34 | 66 | Premotor Cortex | 6 | -28 | 10 | 56 | -3.64 | 53 | |
| Insula | 13 | 34 | -18 | 28 | -4.49 | 24 | Visual Cortex | 18 | -6 | -84 | -4 | -3.59 | 23 | |
| Visual Cortex | 17 | 24 | -70 | 6 | -5.91 | 117 | Time Lag 6 | | | | | | | |
| | 19 | 24 | -84 | 38 | -4.29 | 97 | Positive Correlations | | | | | | | |
| | 18 | -10 | -72 | -6 | -3.78 | 90 | Dorsomedial PFC | 10 | -12 | 62 | 16 | 9.18 | 3629 | |
| | 19 | -20 | -52 | -6 | -3.51 | 27 | 8 | 12 | 48 | 8 | 4.24 | 38 | | |
| | 19 | 14 | -82 | 40 | -3.78 | 24 | Ventromedial PFC | 0 | 11 | 0 | 36 | -28 | 3.47 | 30 |
| | 17 | -28 | -58 | 8 | -3.91 | 23 | Lateral Frontopolar Cortex | 10 | -26 | 60 | -10 | 4.21 | 34 | |
| | 18 | 10 | -78 | 22 | -4.22 | 52 | Ventrolateral PFC | 47 | 32 | 20 | -20 | 8.32 | 1700 | |
| Time Lag 3 | | | | | | | 47 | -52 | 34 | -16 | 6.55 | 298 | | |
| Positive Correlations | | | | | | | Supplementary Motor Area | 6 | -2 | -10 | 58 | 4.44 | 41 | |
| Dorsomedial PFC | 8 | -12 | 34 | 44 | 5.51 | 130 | Anterior Premotor Cortex | 8 | -16 | 36 | 44 | 5.52 | 65 | |
| | 8 | 10 | 26 | 46 | 3.93 | 47 | 8 | 28 | 20 | 26 | 4.43 | 32 | | |
| Lateral Frontopolar Cortex | 10 | -28 | 50 | -14 | 8.08 | 731 | Premotor Cortex | 6 | -52 | -2 | 24 | 8.63 | 3186 | |
| | 10 | 36 | 48 | 8 | 5.51 | 138 | 6 | 40 | -12 | 38 | 5.43 | 73 | | |
| Dorsolateral PFC | 9 | -36 | 26 | 36 | 4.31 | 39 | 6 | 56 | 4 | 24 | 4.32 | 36 | | |
| Ventrolateral PFC | 44 | 62 | 14 | 4 | 7.63 | 1930 | 6 | 22 | -16 | 48 | 4.91 | 21 | | |
| | 11 | -16 | 34 | -22 | 4.15 | 62 | 4 | -54 | -12 | 48 | 5.48 | 231 | | |
| | 11 | -16 | 20 | -16 | 3.56 | 24 | 23 | 14 | -48 | 30 | 4.36 | 27 | | |
| Premotor Cortex | 6 | 30 | -8 | 48 | 3.79 | 26 | 38 | -34 | 10 | -38 | 4.51 | 115 | | |
| Motor Cortex | 4 | -34 | -14 | 44 | 4.34 | 179 | 22 | -64 | -42 | 16 | 5.10 | 104 | | |
| Anterior Premotor Cortex | 8 | 46 | 8 | 50 | 3.87 | 45 | 22 | 44 | -20 | -6 | 4.52 | 30 | | |
| Perirhinal Cortex | 36 | -28 | -6 | -36 | 4.19 | 24 | Middle Temporal Cortex | 22 | 72 | -28 | -2 | 6.55 | 1134 | |
| Insula | 13 | -36 | 0 | 8 | 9.92 | 2116 | 21 | -48 | -12 | -20 | 4.75 | 96 | | |
| Auditory Cortex | 41 | -52 | -16 | 2 | 4.76 | 119 | 20 | 44 | -6 | -24 | 3.79 | 26 | | |
| | 41 | -36 | -26 | 8 | 4.59 | 71 | Hippocampus | 30 | 38 | -10 | -14 | 5.65 | 49 | |
| Middle Temporal Cortex | 21 | -56 | -26 | -18 | 5.60 | 98 | Anterior Cingulate | 24 | -2 | -10 | 34 | 5.61 | 502 | |
| | 21 | 70 | -30 | -12 | 4.15 | 62 | Posterior Cingulate Cortex | 23 | -8 | -40 | 36 | 4.80 | 63 | |
| | 21 | -68 | -32 | -4 | 3.76 | 49 | 1 | 64 | -8 | 16 | 5.41 | 152 | | |
| | 21 | 48 | -38 | -2 | 3.84 | 30 | Inferior Parietal Cortex | 40 | -36 | -40 | 24 | 5.18 | 274 | |
| Inferior Temporal Cortex | 20 | 60 | -26 | -22 | 3.86 | 70 | 39 | 54 | -64 | 40 | 3.74 | 24 | | |
| Middle Cingulate Cortex | 32 | 4 | 12 | 38 | 5.95 | 754 | 39 | -44 | -66 | 50 | 3.54 | 20 | | |
| Superior Parietal Cortex | 7 | -26 | -50 | 70 | 4.81 | 30 | Fusiform Cortex | 37 | 36 | -70 | -14 | 5.23 | 133 | |
| | 7 | 28 | -62 | 64 | 4.27 | 25 | Visual Cortex | 19 | -26 | -80 | 26 | 6.66 | 75 | |
| | 7 | -30 | -50 | 56 | 3.79 | 21 | 19 | -32 | -66 | -16 | 3.94 | 42 | | |
| Inferior Temporal Cortex | 40 | 44 | -44 | 38 | 7.46 | 1028 | 19 | 20 | -74 | 32 | 3.65 | 22 | | |
| | 39 | -52 | -52 | 36 | 7.15 | 468 | Thalamus | 10 | -28 | 14 | 3.81 | 24 | | |
| | 39 | 40 | -64 | 44 | 4.12 | 83 | Cerebellum Lobule VI | -18 | -58 | -18 | 6.04 | 187 | | |
| Fusiform Cortex | 40 | 58 | -18 | 16 | 5.71 | 79 | Negative Correlations | | | | | | | |
| Thalamus | 50 | 8 | -12 | 4 | 4.03 | 22 | Dorsolateral PFC | 46 | -38 | 32 | 20 | -4.04 | 59 | |
| Negative Correlations | | | | | | | Pre-supplementary Motor Area | 6 | 2 | 10 | 52 | -5.64 | 70 | |
| Anterior Cingulate Cortex | 32 | -2 | 26 | -6 | -4.81 | 20 | Premotor Cortex | 6 | -30 | 2 | 44 | -5. | | |

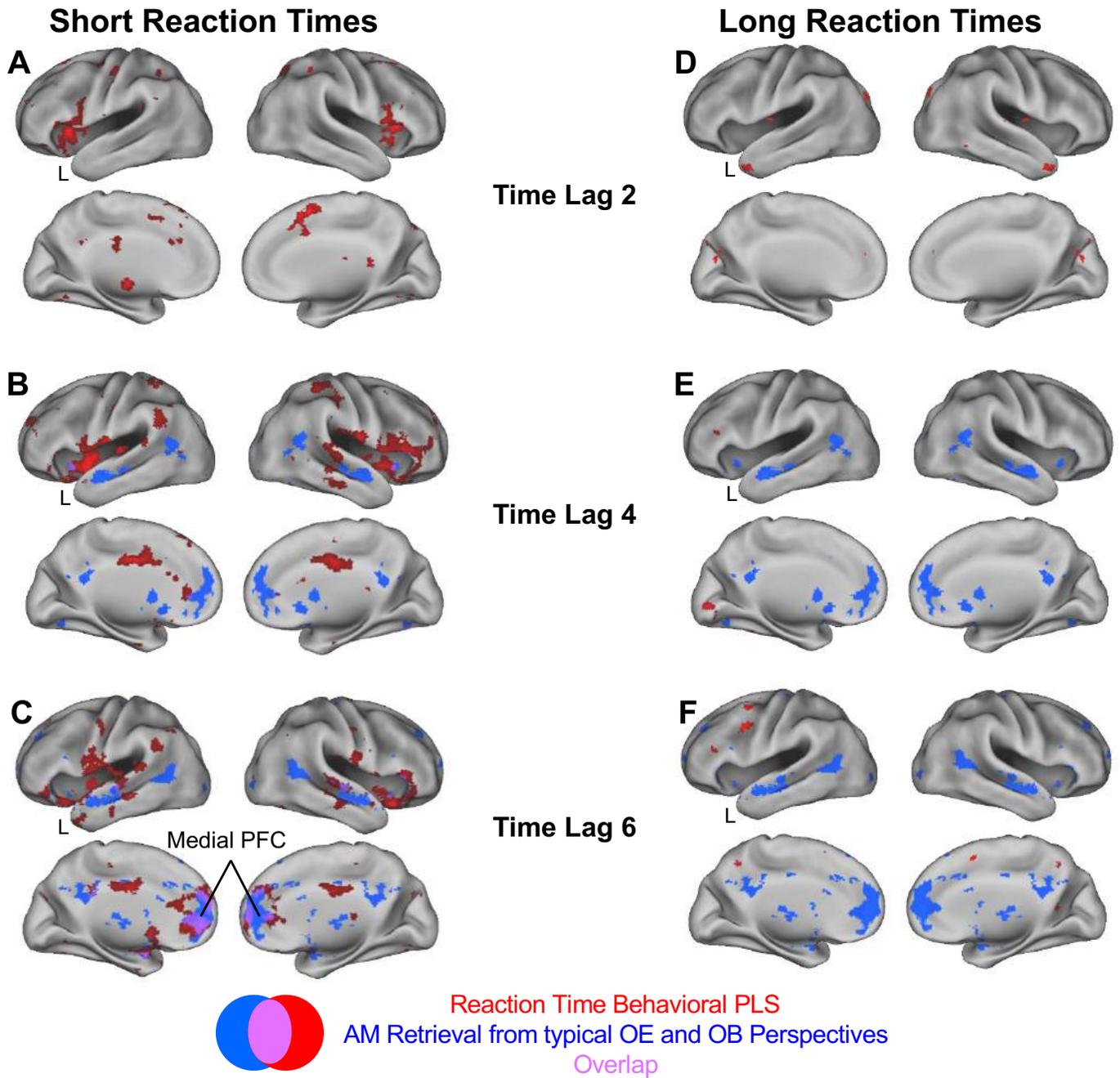


Figure 5. Overlap Between the Spatiotemporal Task PLS and Reaction Time Behavioural PLS. Brain regions identified by the behavioral PLS analyses on the reaction time to construct a memory or visualize a spatial location overlaid onto the pattern of activation associated with AM retrieval from an OE Typical or OB perspective extracted from the spatiotemporal PLS analysis for time lags 2, 4 and 6 for shorter (A to C) and longer (D to F) reaction times. All images depict a BSR threshold of ± 3 .

Second, for perspective maintenance ratings a single significant LV accounted for 40.24% of the variance ($p < .0001$; see Figure 6 and Table 4). Lower perspective maintenance ratings (i.e., positive correlations) were associated with recruitment including left dorsomedial PFC, bilateral visual and temporal cortices, whereas higher perspective maintenance ratings (i.e., negative correlations) were associated with neural recruitment in bilateral medial PFC and precuneus. However, there was minimal overlap for either low or high perspective maintenance ratings and the spatiotemporal PLS (see Figure 7).

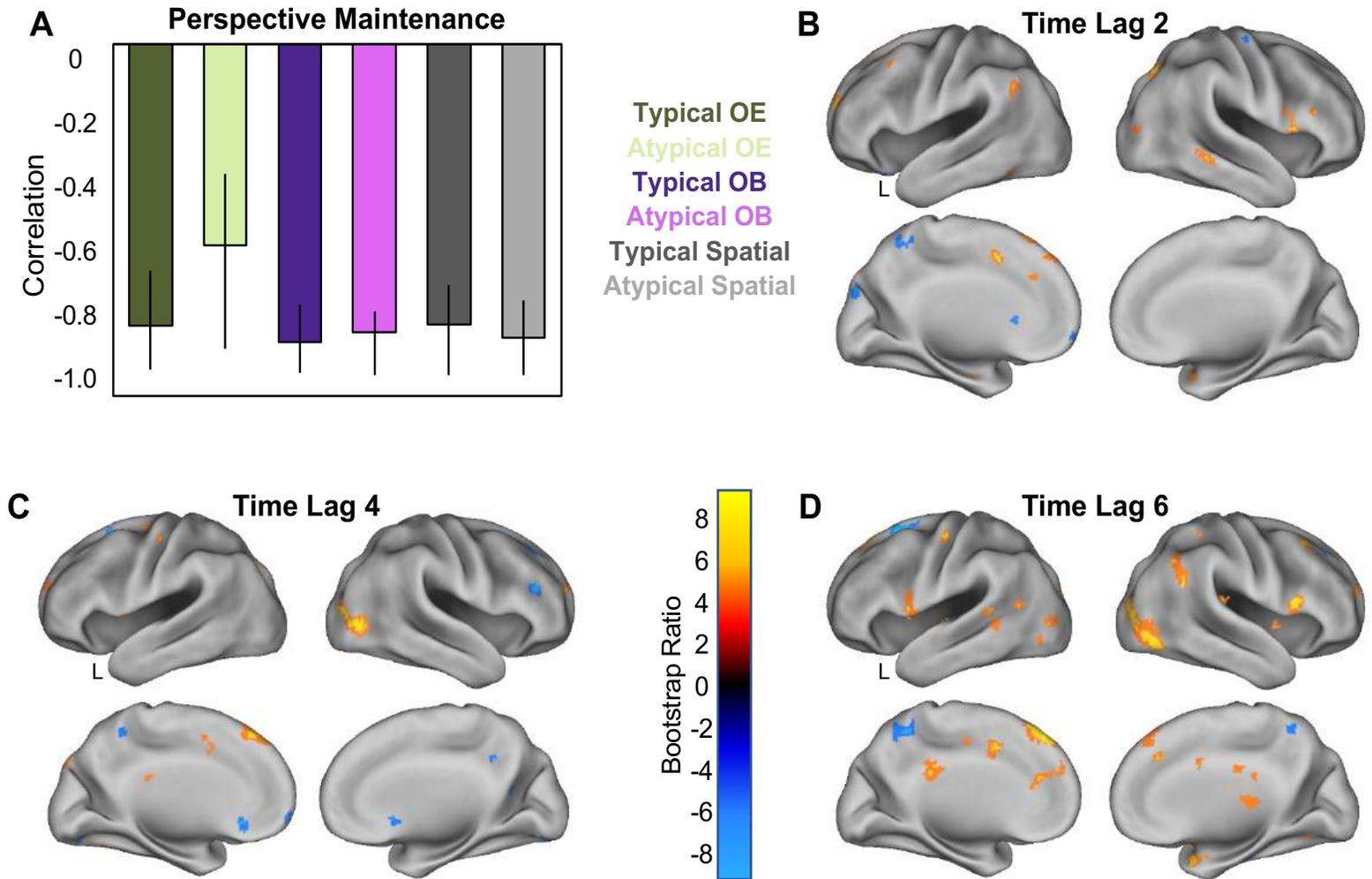


Figure 6 Perspective Maintenance Behavioural PLS. (A) Correlation scores associated with the significant LV from the behavioural PLS on perspective maintenance ratings. Error bars represent the 95% confidence interval, based on bootstrap estimates. Patterns of activation mapped onto the surface of the brain for time lags 2 (B), 4 (C), and 6 (D) are also shown. All images depict a BSR threshold of ± 3 .

| | | | | | | |
|----------------------------------|----|-----|-----|-----|-------|-----|
| | - | - | - | - | - | - |
| Anterior Premotor Cortex | 8 | 36 | 22 | 48 | 5.39 | 72 |
| Premotor Cortex | 6 | -52 | 2 | 2 | 4.88 | 191 |
| | 6 | -32 | -12 | 66 | 5.64 | 180 |
| Motor Cortex | 4 | -52 | -12 | 44 | 3.52 | 23 |
| Insula | 13 | -26 | 26 | 4 | 3.57 | 33 |
| | 13 | 46 | -6 | 0 | 3.90 | 53 |
| Auditory Cortex | 41 | -54 | -28 | 10 | 5.81 | 410 |
| Superior Temporal Cortex | 38 | 32 | 8 | -32 | 5.69 | 275 |
| | 22 | -60 | -46 | 10 | 5.35 | 132 |
| Middle Temporal Cortex | 21 | -70 | -30 | -12 | 4.38 | 50 |
| | 21 | -48 | -16 | -14 | 3.99 | 22 |
| | 21 | 60 | -6 | -18 | 4.13 | 22 |
| Anterior Cingulate Cortex | 23 | 8 | -20 | 34 | 3.80 | 67 |
| Posterior Cingulate Cortex | 23 | -4 | -36 | 34 | 4.31 | 104 |
| Inferior Parietal Cortex | 39 | -42 | -58 | 12 | 6.79 | 209 |
| | 39 | 52 | -60 | 42 | 4.80 | 231 |
| | 40 | 38 | -30 | 18 | 4.60 | 147 |
| Visual Cortex | 19 | 32 | -82 | 16 | 6.81 | 893 |
| | 19 | -26 | -84 | 16 | 6.48 | 222 |
| | 19 | -46 | -84 | 6 | 4.45 | 85 |
| | 19 | 30 | -60 | -6 | 4.65 | 59 |
| | 19 | -32 | -72 | -4 | 4.41 | 44 |
| Thalamus | | 12 | -26 | 12 | 4.18 | 95 |
| Cerebellum Lobule IV, V | | 12 | -46 | -8 | 3.84 | 21 |
| Cerebellum Lobule VI | | 30 | -46 | -28 | 4.87 | 83 |
| Negative Correlations | | | | | | |
| Dorsolateral PFC | 46 | 50 | 42 | 22 | -4.47 | 41 |
| Anterior Premotor Cortex | 8 | 26 | 34 | 40 | -5.51 | 212 |
| Premotor Cortex | 6 | -20 | 16 | 58 | -6.48 | 306 |
| Entorhinal Cortex | 36 | 34 | -24 | -22 | -4.27 | 25 |
| Posterior Parahippocampal Cortex | 36 | -30 | -38 | -8 | -4.76 | 71 |
| Superior Temporal Cortex | 38 | -28 | 18 | -30 | -5.02 | 21 |
| Posterior Cingulate Cortex | 23 | -20 | -52 | 10 | -5.14 | 83 |
| | 23 | 16 | -48 | 20 | -6.39 | 120 |
| Somatosensory Cortex | 5 | -14 | -40 | 60 | -3.94 | 21 |
| Precuneus | 7 | 2 | -52 | 58 | -4.35 | 265 |

PFC = Prefrontal Cortex

Low Perspective Maintenance Ratings

High Perspective Maintenance Ratings

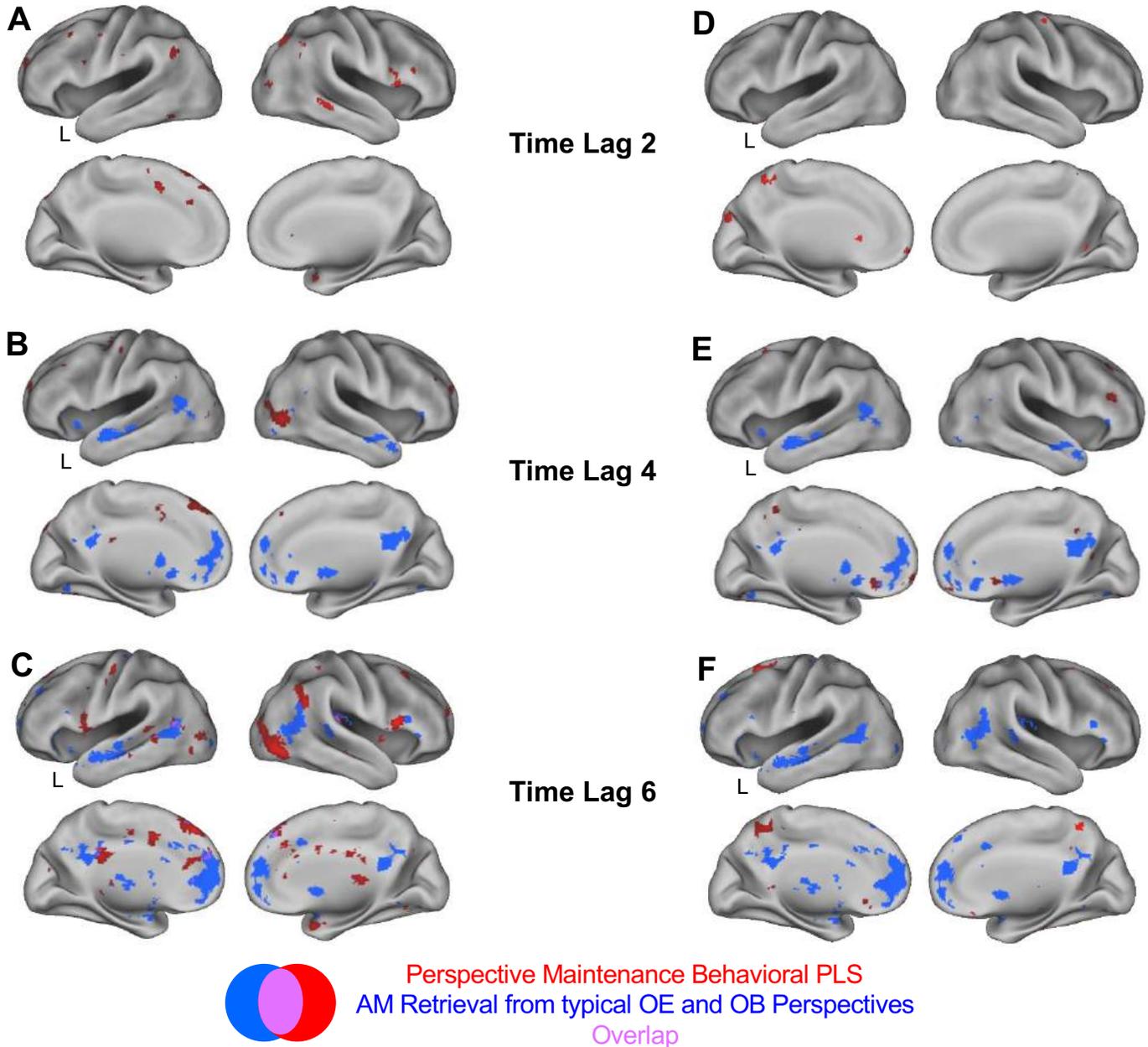


Figure 7. Overlap Between the Spatiotemporal Task PLS and Perspective Maintenance Behavioral PLS. Brain regions identified by the behavioral PLS analyses on perspective maintenance overlaid onto the pattern of activation associated with AM retrieval from an OE same or OB perspective extracted from the spatiotemporal PLS analysis for time lags 2, 4 and 6 for shorter (A to C) and longer (D to F) reaction times. All images depict a BSR threshold of ± 3 .

Third, for vividness ratings a single LV accounted for 36.92% of the variance ($p = .001$; see Figure 8 and Table 5). Lower vividness ratings (i.e., positive correlations) were associated with activity in right posterior parietal and visual cortices, and left parahippocampal cortex, and higher vividness (i.e., negative correlations) with neural recruitment in right precuneus and bilateral medial PFC. There was minimal overlap with the spatiotemporal PLS (see Figure 9).

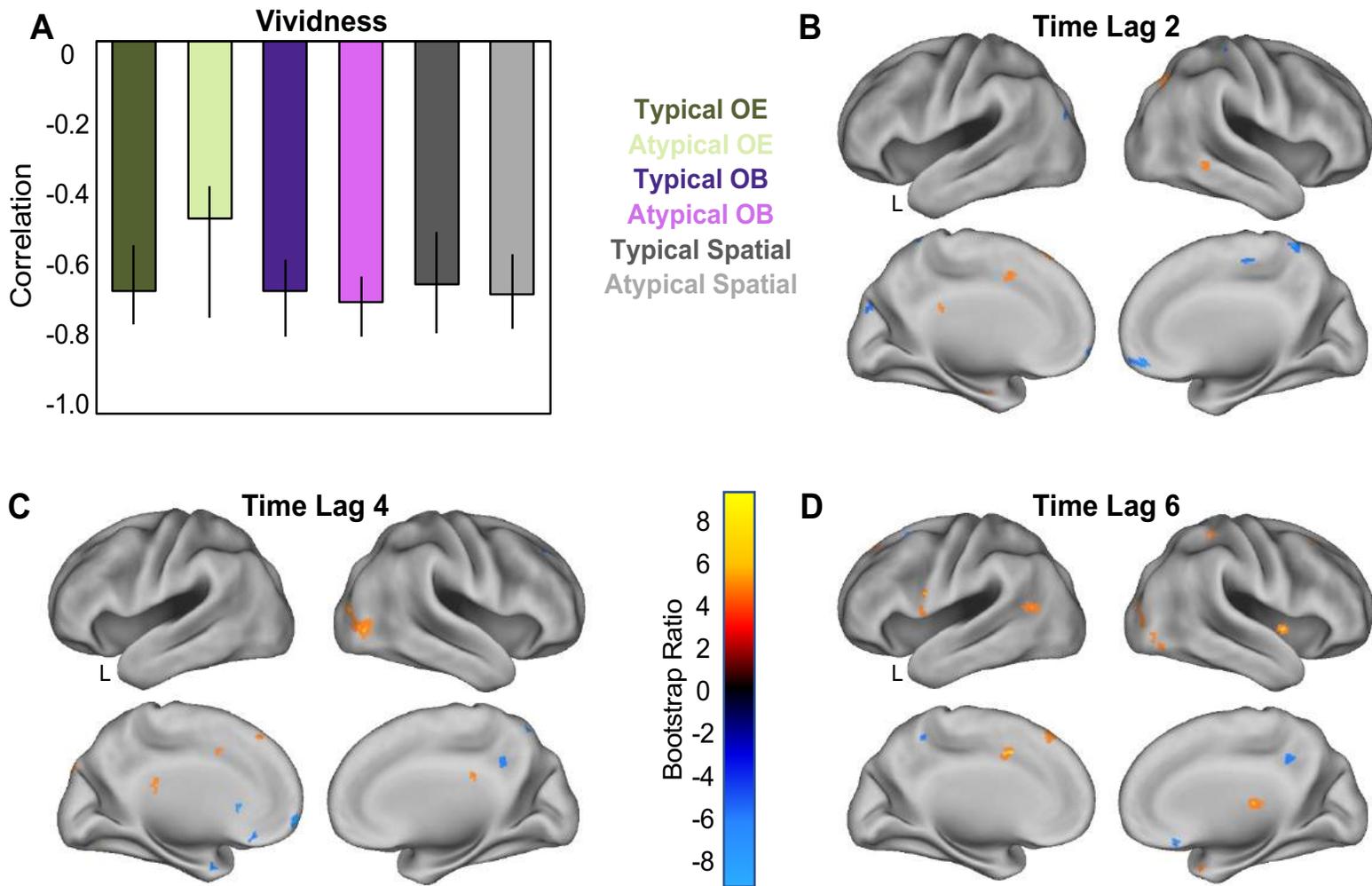


Figure 8. Vividness Behavioural PLS. (A) Correlation scores associated with the significant LV from the behavioural PLS on vividness. Error bars represent the 95% confidence interval, based on bootstrap estimates. Patterns of activation mapped onto the surface of the brain for time lags 2 (B), 4 (C), and 6 (D) are also shown. All images depict a BSR threshold of ± 3 .

Table 5. Behavioural PLS: Vividness

| Region | BA | MNI Coordinates | | | Ratio | Cluster Size | Time Lag 4 | | | | | | |
|------------------------------|----|-----------------|---|---|-------|----------------------------|----------------------------|-----|-----|------|-------|-------|-----|
| | | x | y | z | | | | | | | | | |
| Positive Correlations | | | | | | | Lateral Frontopolar Cortex | 10 | -40 | 44 | 28 | 5.36 | 45 |
| | | | | | | Lateral Frontopolar Cortex | 44 | 66 | 20 | 4 | 5.50 | 52 | |
| | | | | | | Premotor Cortex | 6 | -36 | -4 | 32 | 5.89 | 99 | |
| | | | | | | Premotor Cortex | 6 | -32 | -8 | 66 | 5.84 | 66 | |
| | | | | | | Superior Temporal Cortex | 38 | 40 | 10 | -30 | 4.03 | 36 | |
| | | | | | | Superior Temporal Cortex | 23 | 8 | -30 | 30 | 4.00 | 21 | |
| | | | | | | Visual Cortex | 19 | 44 | -78 | 0 | 4.69 | 219 | |
| | | | | | | Visual Cortex | 19 | -14 | -90 | 38 | 3.51 | 33 | |
| | | | | | | Putamen | 22 | 4 | -6 | 3.94 | 20 | | |
| Negative Correlations | | | | | | | Orbitofrontal Cortex | 10 | -12 | 66 | -12 | -6.95 | 137 |
| | | | | | | Orbitofrontal Cortex | 11 | -14 | 36 | -18 | -4.40 | 97 | |
| | | | | | | Ventromedial PFC | 8 | -24 | 20 | 40 | -6.77 | 109 | |
| | | | | | | Ventrolateral PFC | 8 | 24 | 30 | 38 | -5.99 | 262 | |
| | | | | | | Hippocampus | | -32 | -40 | -2 | -4.25 | 57 | |
| | | | | | | Hippocampus | | 32 | -36 | 2 | -4.16 | 29 | |
| | | | | | | Perirhinal Cortex | 36 | -26 | 4 | -34 | -4.17 | 50 | |
| | | | | | | Inferior Temporal Cortex | 20 | -42 | -22 | -20 | -4.34 | 29 | |
| | | | | | | Posterior Cingulate Cortex | 31 | 12 | -48 | 36 | -4.06 | 34 | |
| | | | | | | Posterior Cingulate Cortex | 39 | -22 | -44 | 34 | -3.90 | 27 | |
| | | | | | | Fusiform Cortex | 37 | 32 | -26 | -24 | -3.82 | 22 | |
| | | | | | | Visual Cortex | 18 | -22 | -82 | -12 | -4.64 | 42 | |
| | | | | | | Visual Cortex | 18 | 18 | -84 | -14 | -3.66 | 29 | |
| Time Lag 5 | | | | | | | Lateral Frontopolar cortex | 10 | 20 | 48 | 10 | 4.12 | 36 |
| | | | | | | Dorsomedial PFC | 8 | -12 | 34 | 54 | 4.19 | 155 | |
| | | | | | | Ventrolateral PFC | 44 | -58 | 8 | 18 | 5.34 | 26 | |
| | | | | | | Premotor Cortex | 6 | -32 | -8 | 66 | 5.77 | 112 | |
| | | | | | | Insula | 13 | 46 | 4 | 4 | 4.44 | 91 | |
| | | | | | | Superior Temporal Cortex | 22 | 62 | 18 | -4 | 4.12 | 24 | |
| | | | | | | Visual Cortex | 19 | 38 | -84 | 8 | 4.85 | 239 | |
| | | | | | | Visual Cortex | 19 | 38 | -66 | -6 | 4.28 | 40 | |
| | | | | | | Thalamus | 19 | -40 | -70 | -2 | 5.03 | 39 | |
| | | | | | | Caudate | | -6 | -26 | 6 | 4.08 | 37 | |
| | | | | | | Caudate | 16 | 22 | 0 | 4.26 | 38 | | |
| Negative Correlations | | | | | | | Ventromedial PFC | 11 | 4 | 26 | -22 | -4.66 | 120 |
| | | | | | | Ventromedial PFC | 10 | -8 | 68 | -8 | -4.67 | 68 | |
| | | | | | | Anterior Premotor Cortex | 8 | -22 | 18 | 42 | -6.09 | 176 | |
| | | | | | | Anterior Premotor Cortex | 8 | 24 | 30 | 38 | -4.70 | 76 | |
| | | | | | | Premotor Cortex | 6 | 18 | -10 | 50 | -4.28 | 23 | |
| | | | | | | Hippocampus | | -30 | -20 | -22 | -4.10 | 63 | |
| | | | | | | Anterior Cingulate Cortex | 32 | -2 | 24 | -10 | -4.46 | 23 | |
| | | | | | | Posterior Cingulate Cortex | 31 | -16 | -48 | 40 | -4.07 | 48 | |
| | | | | | | Posterior Cingulate Cortex | 31 | 10 | -48 | 40 | -4.11 | 45 | |
| | | | | | | Retrosplenial Cortex | 30 | -22 | -50 | 8 | -4.48 | 71 | |
| | | | | | | Precuneus | 7 | -6 | -50 | 56 | -3.47 | 23 | |
| | | | | | | Visual Cortex | 18 | -22 | -80 | -16 | -5.41 | 194 | |
| | | | | | | Visual Cortex | 19 | 24 | -82 | -12 | -4.40 | 73 | |
| Time Lag 6 | | | | | | | Lateral Frontopolar Cortex | 10 | 20 | 48 | 10 | 4.42 | 37 |
| | | | | | | Dorsolateral PFC | 9 | 20 | 46 | 28 | 4.45 | 41 | |
| | | | | | | Ventrolateral PFC | 44 | -62 | 18 | 2 | 3.86 | 46 | |
| | | | | | | Ventrolateral PFC | 44 | -58 | 8 | 6 | 3.57 | 44 | |
| | | | | | | Anterior Premotor Cortex | 44 | -60 | 8 | 20 | 4.87 | 36 | |
| | | | | | | Anterior Premotor Cortex | 8 | -16 | 40 | 48 | 3.68 | 167 | |
| | | | | | | Premotor Cortex | 6 | -32 | -8 | 66 | 5.05 | 69 | |
| | | | | | | Insula | 6 | -40 | 2 | 36 | 4.17 | 30 | |
| | | | | | | Insula | 13 | 46 | -2 | 0 | 5.66 | 113 | |
| | | | | | | Auditory Cortex | 41 | -52 | -30 | 10 | 5.21 | 32 | |
| | | | | | | Auditory Cortex | 41 | 54 | -26 | 10 | 4.05 | 32 | |
| | | | | | | Superior Temporal Cortex | 41 | -48 | -16 | 8 | 3.85 | 28 | |
| | | | | | | Superior Temporal Cortex | 38 | 30 | 14 | -30 | 4.41 | 31 | |
| | | | | | | Inferior Temporal Cortex | 20 | 38 | 4 | -32 | 3.41 | 29 | |
| | | | | | | Anterior Cingulate Cortex | 32 | -12 | 8 | 34 | 6.67 | 103 | |
| | | | | | | Anterior Cingulate Cortex | 24 | 0 | 28 | 22 | 3.74 | 24 | |
| | | | | | | Posterior Cingulate Cortex | 32 | -8 | 38 | 18 | 3.60 | 20 | |
| | | | | | | Posterior Cingulate Cortex | 23 | 16 | -38 | 16 | 4.85 | 165 | |
| | | | | | | Inferior Parietal Cortex | 23 | -12 | -40 | 16 | 4.40 | 42 | |
| | | | | | | Visual Cortex | 39 | -42 | -62 | 12 | 5.02 | 166 | |
| | | | | | | Visual Cortex | 19 | 40 | -74 | -2 | 4.29 | 249 | |
| | | | | | | Visual Cortex | 19 | -26 | -84 | 16 | 3.69 | 45 | |
| | | | | | | Visual Cortex | 19 | 30 | -70 | 16 | 4.23 | 34 | |
| | | | | | | Visual Cortex | 19 | -38 | -70 | -2 | 3.91 | 26 | |
| Negative Correlations | | | | | | | Ventromedial PFC | 11 | 4 | 30 | -20 | -4.36 | 30 |
| | | | | | | Ventromedial PFC | 8 | -22 | 20 | 42 | -4.63 | 201 | |
| | | | | | | Anterior Premotor Cortex | 8 | 22 | 16 | 50 | -4.68 | 52 | |
| | | | | | | Hippocampus | 8 | 20 | 26 | 36 | -4.77 | 28 | |
| | | | | | | Hippocampus | | -30 | -38 | -2 | -6.36 | 54 | |
| | | | | | | Posterior Cingulate Cortex | 31 | -16 | -44 | 40 | -3.85 | 24 | |
| | | | | | | Posterior Cingulate Cortex | 31 | 4 | -48 | 40 | -3.96 | 40 | |
| | | | | | | Precuneus | 7 | -6 | -50 | 56 | -3.50 | 22 | |

PFC = Prefrontal Cortex

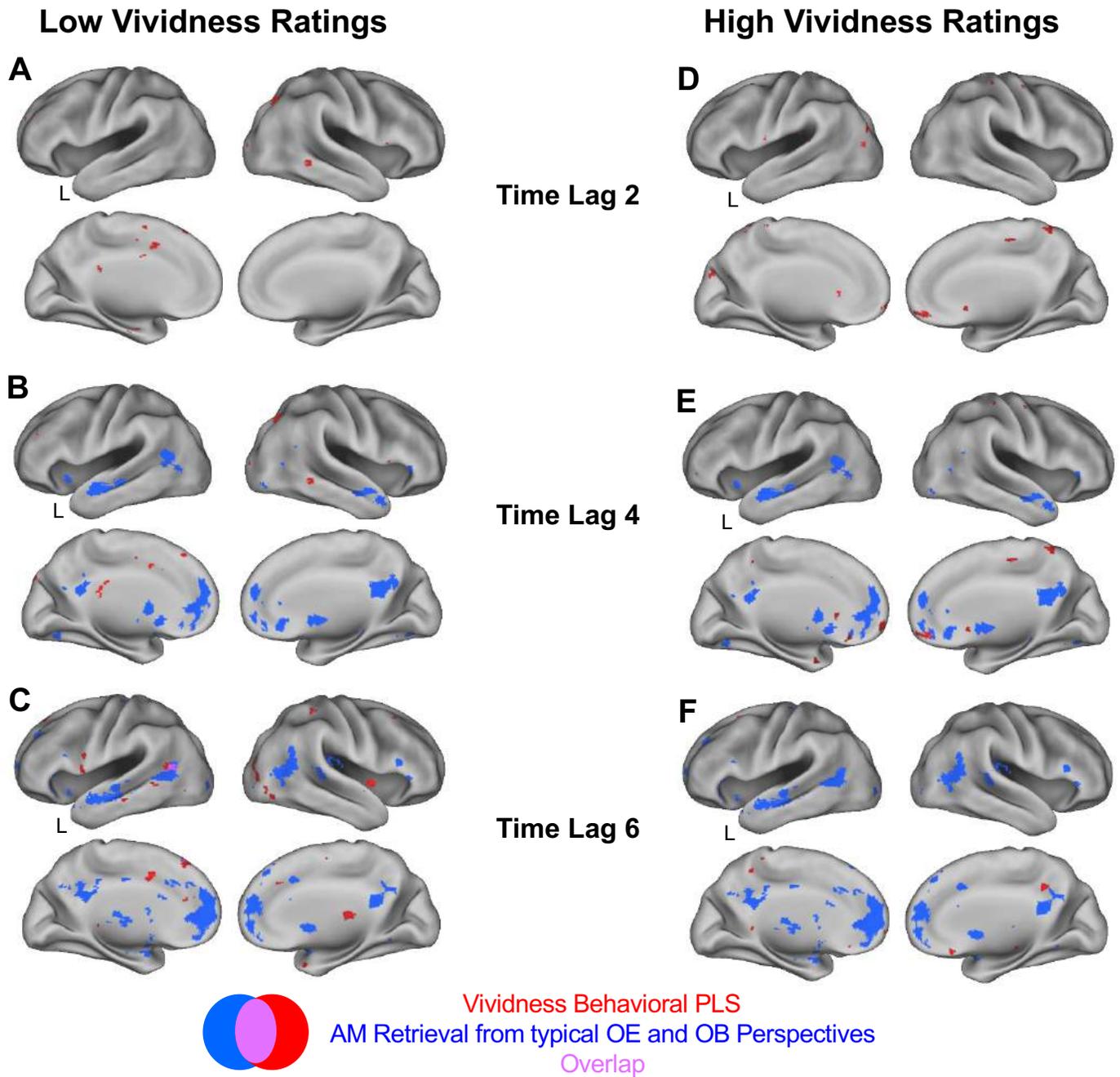


Figure 9. Overlap Between the Spatiotemporal PLS and Vividness Behavioural PLS. Brain regions identified by the behavioral PLS analyses on vividness ratings overlaid onto the pattern of activation associated with AM retrieval from an OE Typical or OB perspective extracted from the spatiotemporal PLS analysis for time lags 2, 4 and 6 for shorter (A to C) and longer (D to F) reaction times. All images depict a BSR threshold of ± 3 .

Fourth, for emotional intensity ratings one significant LV accounted for 35.36% of the variance ($p < .0001$; see Figure 10 and Table 6). Lower emotional intensity ratings were associated with bilateral posterior parietal cortices, dorsolateral PFC, and left precuneus, with minimal overlap with the spatiotemporal PLS (see Figure 11). Higher emotional intensity was associated with right amygdala and insula, as well as bilateral ventrolateral PFC, but there was no overlap with the spatiotemporal PLS.

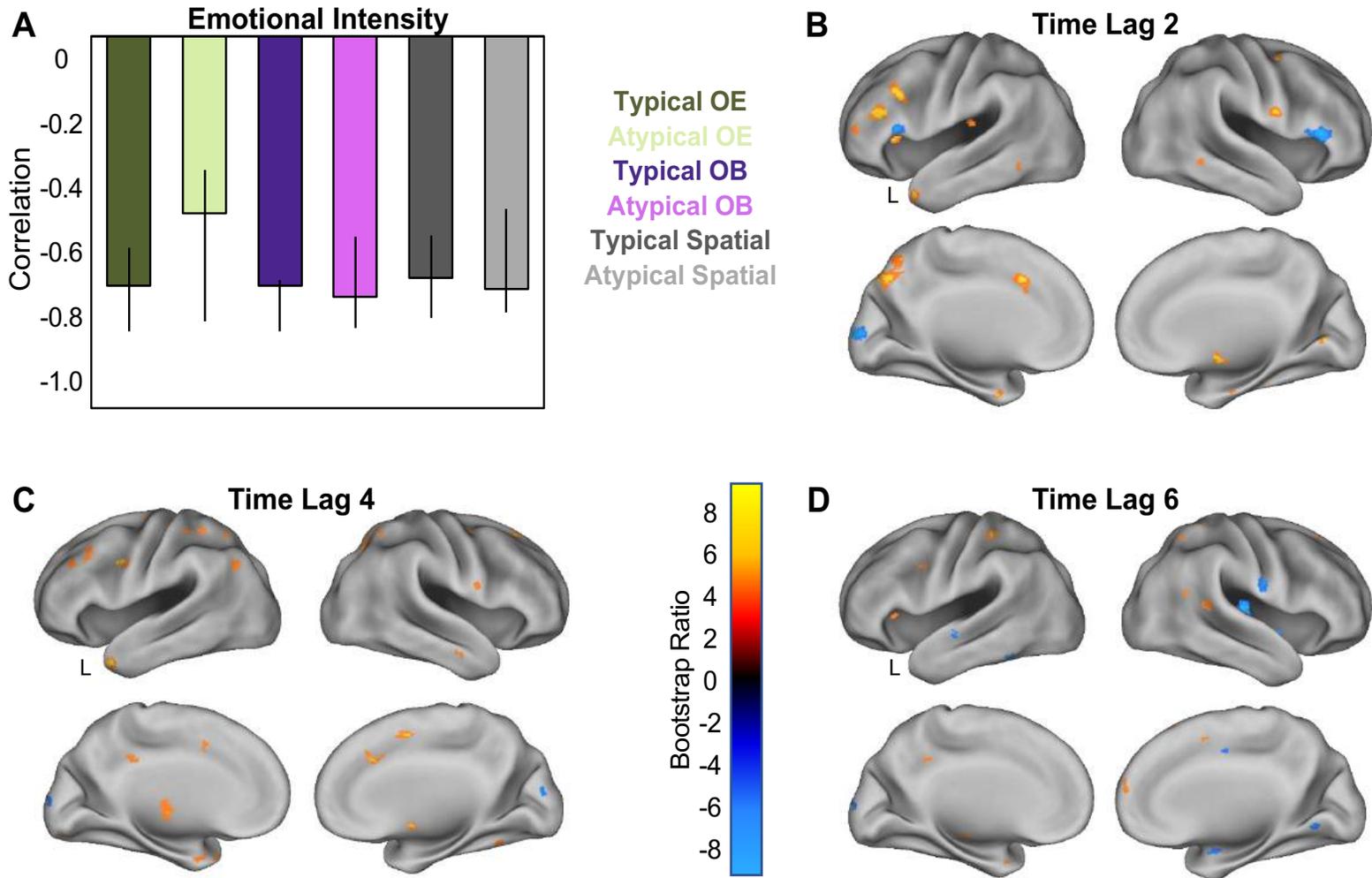
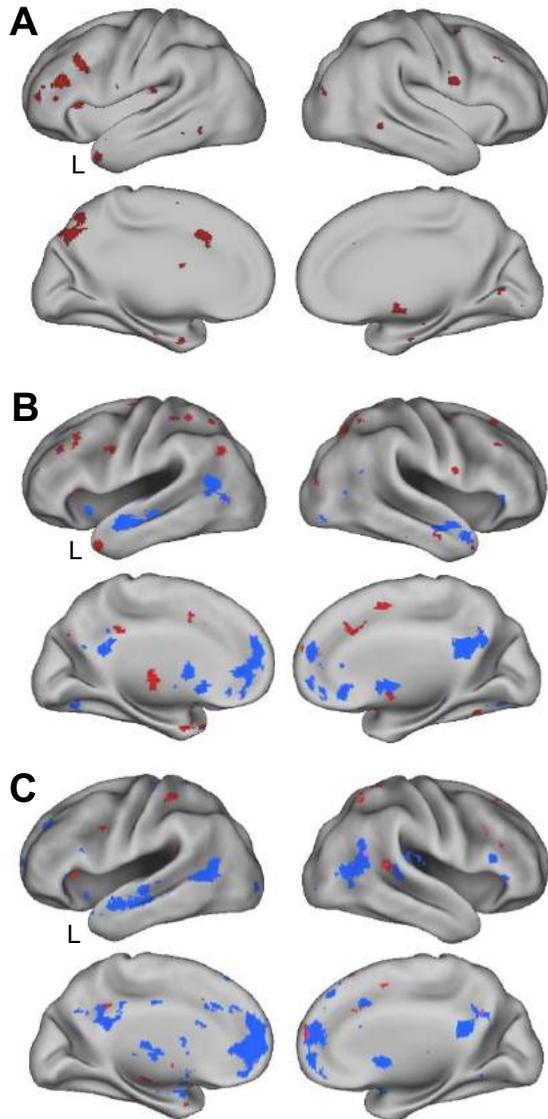


Figure 10. Emotional Intensity Behavioral PLS. (A) Correlation scores associated with the significant LV from the behavioural PLS on emotional intensity. Error bars represent the 95% confidence interval, based on bootstrap estimates. Patterns of activation mapped onto the surface of the brain for time lags 2 (B), 4 (C), and 6 (D) are also shown. All images depict a BSR threshold of ± 3 .

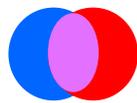
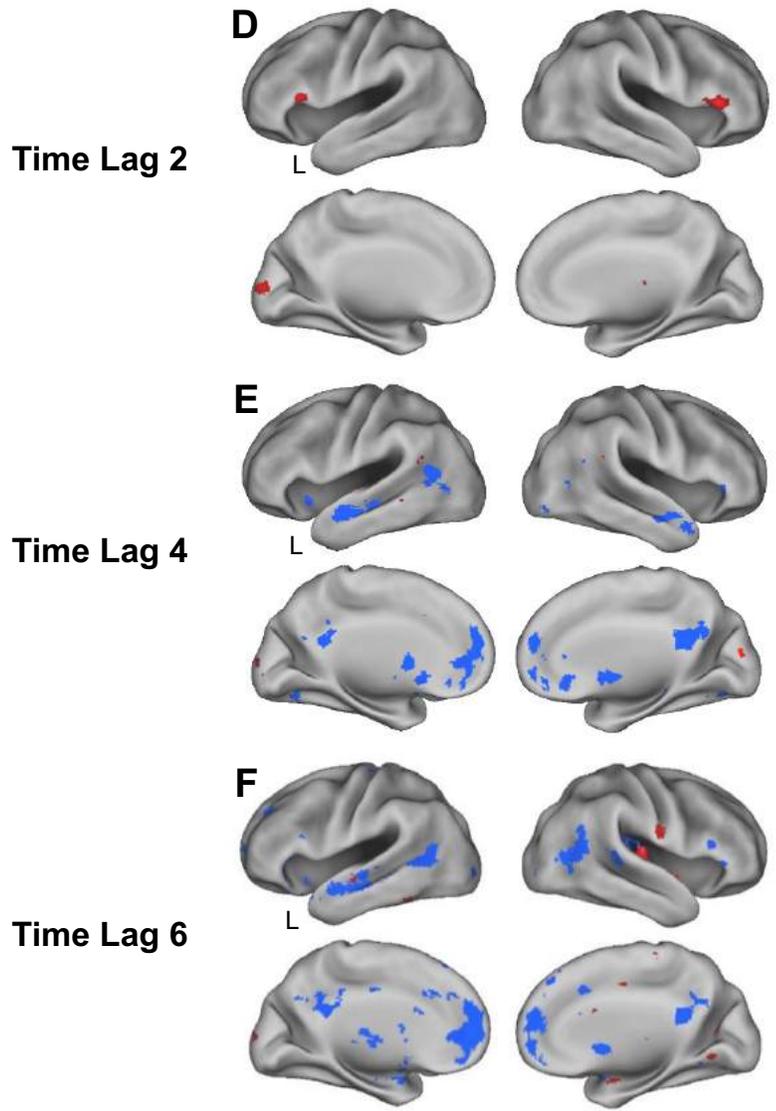
Table 6. Behavioural PLS: Emotional Intensity

| Region | BA | MNI Coordinates | | | Ratio | Cluster Size | Positive Correlations | | | | | Time Lag 4 | | | | | | | | | | | | |
|----------------------------------|----|-----------------|------|------|-------|--------------|----------------------------|--------------------------|-----------------|--------------|--------------------------|-------------------------|----------------------|-----------|--------------------------|--------------------------|-----------------|---------------|----------|---------|----------------------|-----|-------|----|
| | | x | y | z | | | Lateral Frontopolar Cortex | Anterior Premotor Cortex | Premotor Cortex | Motor Cortex | Superior Temporal Cortex | Middle Cingulate Cortex | Somatosensory Cortex | Precuneus | Superior Parietal Cortex | Inferior Parietal Cortex | Fusiform Cortex | Visual Cortex | Thalamus | Putamen | Cerebellum Lobule VI | | | |
| Positive Correlations | | | | | | | Time Lag 1 | | | | | | | | | | | | | | | | | |
| Dorsomedial PFC | 8 | -10 | 18 | 40 | 4.90 | 78 | 10 | -40 | 56 | 16 | 3.99 | 26 | 8 | -48 | 24 | 38 | 4.04 | 111 | 8 | 20 | 30 | 52 | 4.87 | 38 |
| Dorsolateral PFC | 46 | -40 | 42 | 4 | 5.36 | 130 | 6 | -34 | -8 | 56 | 4.78 | 84 | 6 | -18 | -12 | 66 | 4.27 | 82 | 6 | -46 | 2 | 32 | 4.31 | 80 |
| Ventrolateral PFC | 9 | 46 | 28 | 18 | 4.56 | 86 | 6 | 16 | 2 | 50 | 4.47 | 67 | 4 | 66 | 4 | 20 | 5.22 | 29 | 38 | -30 | 8 | -36 | 4.19 | 88 |
| Premotor Cortex | 6 | -26 | 12 | 38 | 4.32 | 54 | 38 | -44 | 14 | -36 | 4.82 | 64 | 38 | -40 | 18 | -30 | 4.41 | 57 | 32 | 14 | 28 | 34 | 4.28 | 63 |
| Auditory Cortex | 41 | 56 | -26 | 8 | 4.10 | 47 | 1 | -38 | -36 | 58 | 3.77 | 70 | 1 | 34 | -34 | 44 | 3.93 | 59 | 7 | -10 | -72 | 38 | 6.18 | 65 |
| Somatosensory Cortex | 1 | -26 | -20 | 38 | 4.19 | 39 | 7 | 26 | -56 | 56 | 5.06 | 281 | 7 | 26 | -56 | 56 | 5.06 | 281 | 40 | -48 | -36 | 40 | 4.76 | 35 |
| Posterior Cingulate Cortex | 23 | 6 | -48 | 16 | 4.08 | 40 | 39 | -46 | -68 | 36 | 3.98 | 24 | 39 | -46 | -68 | 36 | 3.98 | 24 | 37 | 30 | -54 | -18 | 3.54 | 34 |
| Inferior Parietal Cortex | 40 | 42 | -40 | 28 | 4.27 | 29 | 18 | -22 | -86 | 0 | 6.78 | 131 | 19 | 36 | -80 | 16 | 4.16 | 33 | 18 | -32 | -80 | 8 | 4.70 | 21 |
| Fusiform Cortex | 39 | 38 | -64 | 54 | 4.41 | 22 | 18 | -22 | -86 | 0 | 6.78 | 131 | 18 | -32 | -80 | 8 | 4.70 | 21 | 18 | -12 | -12 | 8 | 4.28 | 77 |
| Visual Cortex | 37 | 54 | -46 | -10 | 3.68 | 21 | 18 | -22 | -86 | 0 | 6.78 | 131 | 18 | -32 | -80 | 8 | 4.70 | 21 | 18 | -12 | -12 | 8 | 4.28 | 77 |
| Negative Correlations | | | | | | | Time Lag 2 | | | | | Time Lag 5 | | | | | | | | | | | | |
| Lateral Frontopolar Cortex | 10 | -16 | 42 | -2 | -5.48 | 25 | 10 | -42 | 52 | 6 | 4.26 | 60 | 10 | 8 | 66 | 20 | 4.51 | 48 | 10 | -42 | 52 | 6 | 4.26 | 60 |
| Hippocampus | 20 | -8 | -10 | -10 | -4.22 | 21 | 10 | -42 | 52 | 6 | 4.26 | 60 | 10 | 8 | 66 | 20 | 4.51 | 48 | 10 | -42 | 52 | 6 | 4.26 | 60 |
| Somatosensory Cortex | 1 | -56 | -16 | 36 | -5.49 | 85 | 10 | -42 | 52 | 6 | 4.26 | 60 | 10 | 8 | 66 | 20 | 4.51 | 48 | 10 | -42 | 52 | 6 | 4.26 | 60 |
| Inferior Parietal Cortex | 39 | -40 | -58 | 8 | -5.50 | 83 | 10 | -42 | 52 | 6 | 4.26 | 60 | 10 | 8 | 66 | 20 | 4.51 | 48 | 10 | -42 | 52 | 6 | 4.26 | 60 |
| Visual Cortex | 40 | -64 | -34 | 36 | -4.58 | 68 | 10 | -42 | 52 | 6 | 4.26 | 60 | 10 | 8 | 66 | 20 | 4.51 | 48 | 10 | -42 | 52 | 6 | 4.26 | 60 |
| Visual Association Cortex | 19 | 40 | -72 | 20 | -5.33 | 291 | 10 | -42 | 52 | 6 | 4.26 | 60 | 10 | 8 | 66 | 20 | 4.51 | 48 | 10 | -42 | 52 | 6 | 4.26 | 60 |
| Fusiform Cortex | 18 | -6 | -86 | -12 | -5.66 | 103 | 10 | -42 | 52 | 6 | 4.26 | 60 | 10 | 8 | 66 | 20 | 4.51 | 48 | 10 | -42 | 52 | 6 | 4.26 | 60 |
| Caudate | 37 | 6 | -22 | -32 | -4.20 | 44 | 10 | -42 | 52 | 6 | 4.26 | 60 | 10 | 8 | 66 | 20 | 4.51 | 48 | 10 | -42 | 52 | 6 | 4.26 | 60 |
| Positive Correlations | | | | | | | Time Lag 3 | | | | | Time Lag 6 | | | | | | | | | | | | |
| Lateral Frontopolar Cortex | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Dorsolateral PFC | 46 | -40 | 32 | 20 | 6.45 | 228 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Anterior Premotor Cortex | 8 | -50 | 20 | 34 | 6.15 | 230 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Premotor Cortex | 6 | -32 | 8 | 58 | 4.36 | 62 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Motor Cortex | 6 | 38 | 0 | 52 | 4.44 | 45 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Anterior Cingulate Cortex | 4 | -36 | -6 | 20 | 3.80 | 51 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Entorhinal Cortex | 4 | 66 | 2 | 20 | 4.99 | 104 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Insula | 13 | -28 | 22 | 8 | 4.64 | 123 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Superior Temporal Cortex | 38 | -46 | 14 | -34 | 4.57 | 37 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Middle Temporal Cortex | 21 | -62 | -8 | -16 | 4.86 | 32 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Precuneus | 7 | -10 | -76 | 42 | 4.98 | 255 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Inferior Parietal Cortex | 40 | -48 | -28 | 26 | 3.75 | 43 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Fusiform Cortex | 37 | -62 | -52 | -14 | 3.54 | 31 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Visual Cortex | 37 | 52 | -50 | -10 | 4.07 | 30 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Caudate | 17 | 8 | -70 | 10 | 4.82 | 37 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Pallidum | 12 | 0 | -2 | 5.97 | 63 | 21 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Crus I Lobule of the Cerebellum | 40 | -68 | -32 | 4.89 | 54 | 64 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Crus II Lobule of the Cerebellum | 10 | -76 | -32 | 3.76 | 66 | 64 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Cerebellum Lobule IV, V | -8 | -58 | -20 | 4.11 | 33 | 33 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 | 10 | -30 | 58 | 24 | 4.74 | 61 |
| Negative Correlations | | | | | | | Time Lag 4 | | | | | Time Lag 6 | | | | | | | | | | | | |
| Lateral Frontopolar Cortex | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 |
| Ventrolateral PFC | 45 | -54 | 24 | 8 | -5.47 | 127 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 |
| Visual Cortex | 45 | 54 | 28 | 4 | -6.61 | 248 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 |
| Visual Cortex | 18 | -4 | -100 | 10 | -5.31 | 118 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 |
| Positive Correlations | | | | | | | Time Lag 4 | | | | | Time Lag 6 | | | | | | | | | | | | |
| Dorsomedial PFC | 8 | 12 | 24 | 32 | 5.71 | 46 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 |
| Lateral Frontopolar Cortex | 10 | -38 | 52 | 12 | 4.12 | 59 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 |
| Dorsolateral PFC | 10 | 16 | 42 | 12 | 4.70 | 42 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 |
| Anterior Premotor Cortex | 9 | -36 | 30 | 22 | 5.42 | 41 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 |
| Premotor Cortex | 8 | -52 | 18 | 36 | 6.06 | 153 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 |
| Motor Cortex | 8 | 24 | 30 | 52 | 5.60 | 88 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 |
| Inferior Parietal Cortex | 6 | 30 | -12 | 58 | 6.00 | 213 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 |
| Superior Temporal Cortex | 6 | -34 | 8 | 60 | 6.07 | 143 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 |
| Middle Temporal Cortex | 6 | -56 | 0 | 28 | 3.72 | 49 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 |
| Insula | 6 | -30 | -18 | 60 | 3.54 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 |
| Superior Temporal Cortex | 4 | 56 | -12 | 38 | 3.85 | 22 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 |
| Middle Temporal Cortex | 4 | -54 | -14 | 46 | 3.69 | 20 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 |
| Insula | 4 | 64 | -2 | 36 | 4.66 | 20 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 | 10 | 14 | 62 | -10 | -4.92 | 39 |
| Superior Temporal Cortex | 13 | -28 | 24 | 8 | 5.17 | 77 | 10 | 14 | | | | | | | | | | | | | | | | |

Low Emotional Intensity Ratings



High Emotional Intensity Ratings



Emotional Intensity Behavioral PLS
 AM Retrieval from typical OE and OB Perspectives
 Overlap

Figure 11. *Overlap Between the Spatiotemporal PLS and Emotional Intensity Behavioral PLS.* Brain regions identified by the behavioral PLS analyses on emotional intensity ratings overlaid onto the pattern of activation associated with AM retrieval from an OE same or OB perspective extracted from the spatiotemporal PLS analysis for time lags 2, 4 and 6 for shorter (A to C) and longer (D to F) reaction times. All images depict a BSR threshold of ± 3 .

In sum, I found minimal neural overlap in the pattern of activation contributing to behavior when compared to the pattern of activation from the spatiotemporal task-related PLS analysis, suggesting that behavioral differences in reaction time and subjective ratings do not fully account for the patterns of activation that distinguished AM retrieval from typical OE or atypical OB Perspectives.

2.4.4. Hippocampal Seed PLS

I conducted a seed PLS analysis to examine whether functional connectivity with the left anterior hippocampus, which was recruited in both the typical OE and OB conditions, was sensitive to differences in visual perspective during construction and elaboration of autobiographical memories. Four significant LVs were found. LV1 (27.78% of variance, $p = .001$; see Figure 2 and Table 2 in Appendix A) and LV4 (2.39% of variance, $p = .01$; see Figure 3 and Table 3 in Appendix A) did not differentiate among the conditions. In contrast, LV2 (9.59% of variance, $p = .03$; Figure 4A in Appendix A) distinguished the atypical OB condition (i.e. positive correlations) from the typical OE condition (i.e. negative correlations). LV3 (10.93% of variance, $p = .006$; see Figure 4B in Appendix A) distinguished the typical spatial condition (i.e. positive correlations) from both OB conditions (i.e. negative correlations). The temporal pattern in both LV2 and LV3 peaked at time lag 1 (i.e., during construction) and differences between the conditions persisted across the remaining time lags (i.e., during elaboration; see Figure 4C&D in Appendix A).

First, turning to differences between atypical OB and typical OE conditions shown in LV2 (see Table 7), there was greater hippocampal functional connectivity with left precuneus, angular gyrus, thalamus, right retrosplenial cortex, and bilateral posterior parahippocampal cortices during construction (i.e. time lag 1; see Figure 12). Notably, these regions belong to a posterior medial network (Ranganath & Ritchey 2012), which is linked to the translation of stored memory traces within the hippocampus to egocentric representations during long-term memory retrieval (Byrne et al. 2007). In contrast, in the typical OE condition there was greater hippocampal functional connectivity with bilateral superior temporal cortex, likely reflective of increased access to stored semantic information as the retrieved memory was reconstructed (Binder & Desai 2011; Maguire, Mummery, & Büchel, 2000; Svoboda, McKinnon, & Levine, 2006).

Table 7. Hippocampus Seed PLS LV2

| Region | BA | MNI Coordinates | | | Ratio | Cluster Size |
|----------------------------------|----|-----------------|-----|-----|-------|--------------|
| | | x | y | z | | |
| Time Lag 1 | | | | | | |
| Positive Correlations | | | | | | |
| Lateral Frontopolar Cortex | 10 | -26 | 42 | 16 | 6.24 | 556 |
| | 10 | 18 | 54 | -6 | 6.30 | 152 |
| Ventrolateral PFC | 47 | -42 | 18 | 0 | 4.69 | 217 |
| Premotor Cortex | 6 | -36 | -16 | 64 | 6.05 | 108 |
| | 6 | -48 | -8 | 4 | 5.81 | 85 |
| | 6 | -34 | -2 | 32 | 4.64 | 53 |
| | 6 | -16 | 26 | 58 | 4.72 | 27 |
| | 6 | 50 | 4 | 30 | 4.75 | 24 |
| Motor Cortex | 4 | -36 | -20 | 46 | 3.93 | 21 |
| Auditory Cortex | 41 | 38 | -34 | 12 | 6.75 | 59 |
| Posterior Parahippocampal Cortex | 36 | 20 | -30 | -18 | 5.07 | 63 |
| | 36 | -14 | -30 | -12 | 4.59 | 28 |
| Precuneus | 7 | -4 | -54 | 68 | 4.99 | 88 |
| | 7 | -6 | -66 | 38 | 4.45 | 44 |
| Retrosplenial Cortex | 30 | 2 | -38 | 24 | 4.17 | 35 |
| Inferior Parietal Cortex | 40 | 46 | -28 | 36 | 6.81 | 382 |
| | 39 | -52 | -48 | 18 | 5.39 | 121 |
| | 40 | -42 | -22 | 34 | 3.77 | 44 |
| Visual Cortex | 19 | -48 | -68 | 10 | 6.22 | 74 |
| | 19 | 16 | -74 | 36 | 4.85 | 62 |
| Thalamus | | -8 | -26 | 16 | 8.53 | 849 |
| Pallidum | | -16 | -2 | 6 | 4.45 | 59 |
| Putamen | | 22 | 4 | 8 | 5.78 | 61 |
| Crus I Lobule of the Cerebellum | | 40 | -68 | -28 | 3.73 | 29 |
| Cerebellum Lobule IV, V | | 16 | -50 | -20 | 6.26 | 39 |
| Vermis | | 4 | -66 | -12 | 3.93 | 41 |
| Negative Correlations | | | | | | |
| Dorsolateral PFC | 9 | 50 | 38 | 26 | -4.01 | 146 |
| | 46 | 50 | 46 | 12 | -6.97 | 90 |
| | 47 | 42 | 26 | -22 | -3.76 | 22 |
| Premotor Cortex | 6 | -46 | -8 | 18 | -4.52 | 29 |
| Somatosensory Cortex | 1 | -44 | -22 | 22 | -4.01 | 28 |
| | 1 | 44 | -12 | 20 | -3.97 | 30 |
| Anterior Cingulate Cortex | 32 | -2 | 30 | -8 | -3.45 | 25 |
| | 32 | 6 | 40 | -2 | -4.30 | 21 |
| Posterior Parahippocampal Cortex | 36 | -34 | -34 | -20 | -4.83 | 24 |
| Superior Temporal Cortex | 38 | -30 | 14 | -32 | -4.32 | 111 |
| | 22 | 44 | -30 | 2 | -7.23 | 86 |
| | 38 | 38 | 14 | -40 | -4.73 | 40 |
| | 22 | 68 | -14 | -10 | -3.84 | 26 |
| Inferior Temporal Cortex | 20 | 54 | -6 | -38 | -4.36 | 65 |
| | 20 | 40 | -4 | -38 | -4.54 | 48 |
| Inferior Parietal Cortex | 40 | -44 | -22 | -22 | -4.01 | 28 |
| Fusiform Cortex | 37 | 50 | -52 | 14 | -6.75 | 91 |
| Visual Cortex | 17 | 10 | -76 | 14 | -5.41 | 44 |
| | 19 | 28 | -76 | -4 | -6.13 | 43 |
| Caudate | | 12 | 12 | 18 | -7.80 | 169 |
| Crus I Lobule of the Cerebellum | | -30 | -78 | -20 | -4.39 | 20 |
| Time Lag 2 | | | | | | |
| Positive Correlations | | | | | | |
| Dorsomedial PFC | 9 | -8 | 48 | 42 | 4.08 | 66 |
| | 8 | 6 | 22 | 58 | 4.22 | 50 |
| Lateral Frontopolar Cortex | 10 | -26 | 48 | 14 | 5.43 | 198 |
| | 10 | 38 | 54 | 8 | 3.51 | 30 |
| Ventrolateral PFC | 47 | -46 | 34 | -8 | 5.33 | 167 |
| | 47 | -40 | 18 | -10 | 4.66 | 78 |
| | 45 | -60 | 26 | 6 | 6.61 | 140 |
| | 44 | 48 | 18 | 0 | 4.42 | 185 |
| Premotor Cortex | 6 | -34 | -14 | 66 | 5.34 | 148 |
| Insula | 13 | 40 | 0 | 8 | 4.63 | 36 |
| Somatosensory Cortex | 1 | -38 | -24 | 36 | 4.59 | 43 |
| Precuneus | 7 | 6 | -68 | 54 | 4.49 | 91 |
| Superior Parietal Cortex | 7 | 30 | -42 | 42 | 4.50 | 87 |
| Inferior Parietal Cortex | 40 | 44 | -30 | 36 | 5.70 | 510 |
| | 39 | -40 | -58 | 10 | 5.14 | 36 |
| | 39 | -46 | -54 | 26 | 4.62 | 32 |
| | 40 | -54 | -20 | 34 | 4.80 | 31 |
| Visual Cortex | 19 | 46 | -72 | 2 | 3.72 | 30 |
| | 19 | -46 | -70 | 8 | 4.63 | 21 |
| Caudate | 48 | -18 | -20 | 20 | 4.56 | 22 |
| Negative Correlations | | | | | | |
| Ventromedial PFC | 10 | 8 | 42 | -4 | -4.52 | 228 |
| Ventrolateral PFC | 44 | -44 | 14 | 28 | -5.75 | 269 |
| Hippocampus | | -24 | -28 | -4 | -4.33 | 136 |
| | | 32 | -26 | -14 | -5.63 | 125 |
| Superior Temporal Cortex | 38 | -26 | 14 | -28 | -4.70 | 79 |
| | 38 | -44 | 12 | -40 | -4.41 | 40 |
| Middle Temporal Cortex | 21 | -54 | -40 | -2 | -5.43 | 146 |
| | 21 | -54 | -4 | -14 | -4.28 | 50 |
| Inferior Temporal Cortex | 20 | 40 | -6 | -40 | -6.26 | 136 |
| Somatosensory Cortex | 5 | -20 | -34 | 40 | -5.00 | 146 |
| Inferior Parietal Cortex | 7 | -16 | -70 | 34 | -6.42 | 683 |
| | 7 | -26 | -72 | 36 | -5.45 | 189 |
| Posterior Cingulate Cortex | 31 | -20 | -34 | 40 | -5.00 | 146 |
| Fusiform Cortex | 37 | -30 | -48 | -10 | -4.58 | 79 |
| | 37 | 32 | -62 | -8 | -4.60 | 44 |
| Visual Cortex | 17 | 10 | -74 | 12 | -8.38 | 1147 |
| | 18 | 22 | -74 | -8 | -5.19 | 248 |
| | 18 | -18 | -92 | -4 | -5.48 | 212 |
| | 19 | -44 | -76 | 22 | -5.10 | 80 |
| | 19 | 32 | -62 | 34 | -5.12 | 64 |
| | 19 | 26 | -80 | 22 | -6.38 | 54 |
| | 17 | 30 | -56 | 10 | -4.53 | 26 |
| | 19 | -26 | -70 | -4 | -4.04 | 23 |
| Crus I Lobule of the Cerebellum | | -38 | -50 | -36 | -4.84 | 41 |
| Time Lag 3 | | | | | | |
| Positive Correlations | | | | | | |
| Lateral Frontopolar Cortex | 10 | 18 | 50 | 20 | 4.14 | 28 |
| Ventrolateral PFC | 44 | 54 | 16 | 8 | 4.48 | 100 |
| | 47 | -56 | 32 | -10 | 4.67 | 41 |
| | 47 | -42 | 22 | -10 | 4.19 | 29 |
| Premotor Cortex | 6 | 38 | -2 | 32 | 5.19 | 47 |
| Insula | 13 | -34 | 8 | 6 | 3.98 | 44 |
| Auditory Cortex | 41 | -44 | -26 | 8 | 4.81 | 57 |
| Superior Temporal Cortex | 22 | 62 | -30 | 12 | 5.21 | 108 |
| | 22 | 48 | 2 | -10 | 4.40 | 26 |
| Superior Parietal Cortex | 7 | -28 | -52 | 52 | 4.26 | 31 |
| | 7 | 22 | -54 | 52 | 4.01 | 38 |
| Inferior Parietal Cortex | 40 | 44 | -34 | 50 | 5.35 | 200 |
| | 40 | -36 | -40 | 44 | 4.52 | 32 |
| | 40 | 50 | -26 | 38 | 3.48 | 20 |
| Visual Cortex | 19 | 44 | -72 | 2 | 4.27 | 56 |
| | 18 | -16 | -92 | 26 | 5.49 | 48 |
| Thalamus | | -20 | -22 | 6 | 5.91 | 38 |
| Negative Correlations | | | | | | |
| Ventromedial PFC | 11 | -2 | 28 | -10 | -5.72 | 109 |
| Ventrolateral PFC | 44 | -44 | 16 | 30 | -5.47 | 282 |
| Supplementary Motor Area | 6 | -6 | 12 | 52 | -4.18 | 61 |
| Anterior Premotor Cortex | 8 | 38 | 8 | 38 | -4.51 | 45 |
| | 8 | 22 | 36 | 42 | -3.84 | 30 |
| Premotor Cortex | 6 | 22 | 4 | 50 | -6.33 | 347 |
| | 6 | -18 | -22 | 68 | -4.79 | 84 |
| | 6 | -20 | 14 | 58 | -4.27 | 61 |
| Amygdala | 34 | -30 | 2 | -20 | -3.67 | 29 |
| Hippocampus | | 32 | -28 | -8 | -5.60 | 149 |
| Posterior Parahippocampal Cortex | 36 | -28 | -40 | -10 | -5.19 | 272 |
| Superior Temporal Cortex | 38 | 34 | 14 | -42 | -4.35 | 26 |
| Middle Temporal Cortex | 21 | -56 | -10 | -18 | -4.07 | 53 |
| | 21 | -52 | -42 | -4 | -4.51 | 23 |
| Somatosensory Cortex | 1 | -42 | -18 | 26 | -7.34 | 69 |
| Posterior Cingulate Cortex | 31 | 16 | -48 | 46 | -5.16 | 40 |
| | 23 | -18 | -52 | 12 | -9.64 | 2082 |
| Precuneus | 7 | 12 | -50 | 60 | -4.21 | 37 |
| Sensory Association Cortex | 5 | -24 | -36 | 64 | -4.80 | 24 |
| | 5 | 12 | -32 | 52 | -4.40 | 32 |
| Inferior Parietal Cortex | 39 | 40 | -76 | 38 | -4.84 | 176 |
| Fusiform Cortex | 37 | -50 | -54 | -4 | -4.13 | 60 |
| Visual Cortex | 19 | -44 | -76 | 22 | -5.24 | 238 |
| | 18 | -16 | -90 | -2 | -5.11 | 178 |
| | 18 | -8 | -84 | -8 | -3.59 | 63 |
| | 18 | -30 | -84 | -6 | -4.79 | 43 |
| Putamen | | -22 | -10 | 16 | -6.08 | 59 |
| Vermis of the Cerebellum | | 6 | -56 | -36 | -4.48 | 153 |
| Crus I Lobule of the Cerebellum | | -44 | -48 | -34 | -4.31 | 54 |
| | | -36 | -60 | -36 | -4.06 | 37 |
| | | -24 | -64 | -34 | -3.66 | 30 |
| Crus II Lobule of the Cerebellum | | 8 | -76 | -32 | -4.17 | 63 |
| Cerebellum Lobule VI | | 26 | -54 | -32 | -3.73 | 21 |
| Time Lag 4 | | | | | | |
| Positive Correlations | | | | | | |
| Ventrolateral PFC | 47 | -40 | 22 | -12 | 4.68 | 70 |
| Ventral Anterior Premotor Cortex | 44 | -58 | 8 | 16 | 4.53 | 33 |
| Premotor Cortex | 6 | -36 | -14 | 66 | 6.87 | 36 |
| Superior Temporal Cortex | 21 | 70 | -10 | -18 | 5.81 | 73 |
| | 22 | -48 | -10 | -4 | 4.92 | 50 |
| | 22 | -48 | -36 | 12 | 4.57 | 34 |
| Auditory Cortex | 41 | -38 | -20 | 4 | 3.59 | 23 |
| Insula | 13 | -34 | 10 | 2 | 4.64 | 145 |
| | 13 | 32 | 20 | -14 | 5.82 | 47 |
| | 13 | 48 | 2 | -4 | 3.67 | 25 |
| Somatosensory Cortex | 1 | 58 | -10 | 16 | 3.74 | 32 |
| | 1 | -58 | -16 | 12 | 5.17 | 22 |
| Middle Cingulate Cortex | 24 | -14 | -10 | 46 | 5.85 | 28 |
| Retrosplenial Cortex | 30 | 24 | -42 | 6 | 4.22 | 31 |
| Superior Parietal Cortex | 7 | -32 | -48 | 54 | 3.71 | 48 |
| Inferior Parietal Cortex | 40 | 46 | -34 | 40 | 4.48 | 122 |
| Visual Cortex | 18 | -14 | -92 | 28 | 4.89 | 63 |
| Thalamus | | -14 | -24 | 18 | 5.80 | 42 |
| | | 2 | -12 | 14 | 5.44 | 21 |
| Putamen | | -28 | -66 | 4 | 3.93 | 79 |
| | | 22 | 20 | 4 | -4.30 | 25 |
| Negative Correlations | | | | | | |
| Ventromedial PFC | 10 | -4 | 54 | -10 | -3.54 | 42 |
| Ventrolateral PFC | 11 | -22 | 38 | -20 | -4.02 | 28 |
| Lateral Frontopolar Cortex | 10 | -26 | 56 | 6 | -3.89 | 37 |
| | 46 | -32 | 34 | 10 | -4.73 | 24 |
| Dorsolateral PFC | 9 | 58 | 32 | 14 | -3.71 | 207 |

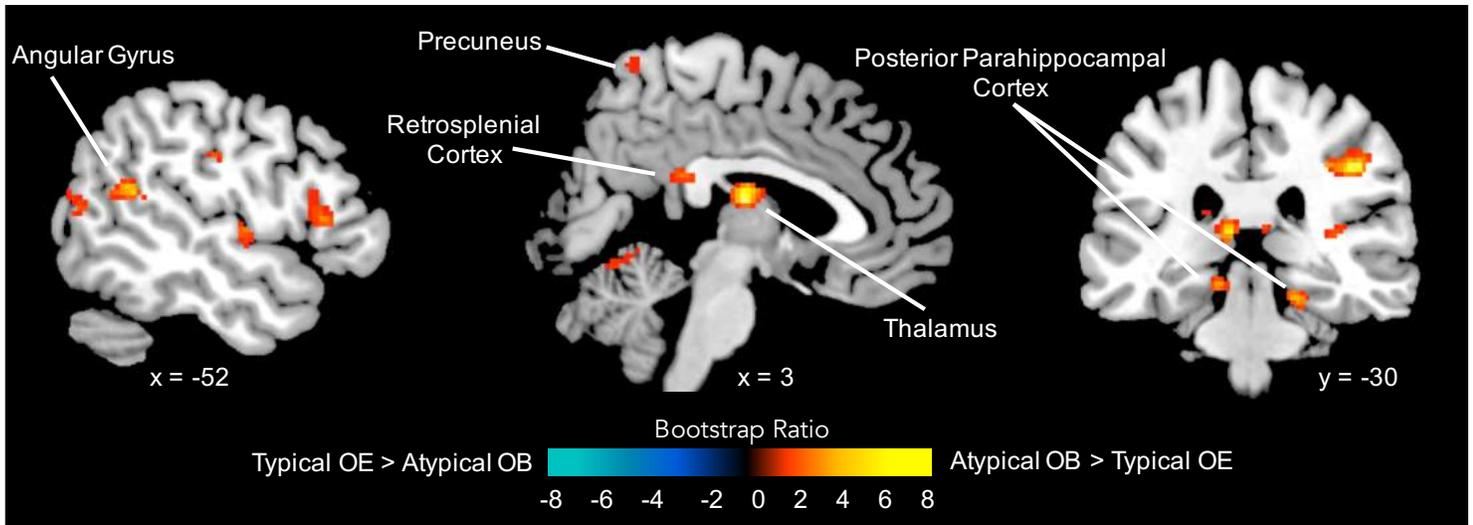


Figure 12. Hippocampus Functional Connectivity During Construction. The pattern of functional connectivity with the left anterior hippocampus identified in LV2 showing differences between the typical OE and atypical OB conditions during construction (i.e., time lag 1). All images depict a BSR threshold of ± 3

During later phases of retrieval (i.e. time lags 3 to 6), there was greater hippocampal functional connectivity with an extended MTL network, including MTL regions as well as ventromedial PFC and visual cortices for autobiographical memories retrieved from typical OE compared to atypical OB perspectives (see Figure 13). Specifically, the left anterior hippocampus exhibited greater functional connectivity with right hippocampus, distinct sub-regions of the ipsilateral hippocampus, and posterior parahippocampal cortices, as well as left amygdala and entorhinal cortex, suggesting greater integration within an MTL network when elaborating upon autobiographical memories from typical OE perspectives (see Figure 5 in Appendix C). In contrast, when elaborating upon autobiographical memories from atypical OB perspectives there was greater hippocampal functional connectivity with dorsomedial PFC (i.e., during time lags 2, 5, and 6; see Table 7). Additionally, there was a reversal in the pattern of hippocampal connectivity with

the precuneus during elaboration in the typical OE and atypical OB conditions. As retrieval progressed from construction to elaboration functional connectivity between the hippocampus and precuneus became stronger in the typical OE compared to atypical OB conditions (i.e., time lags 3 to 6).

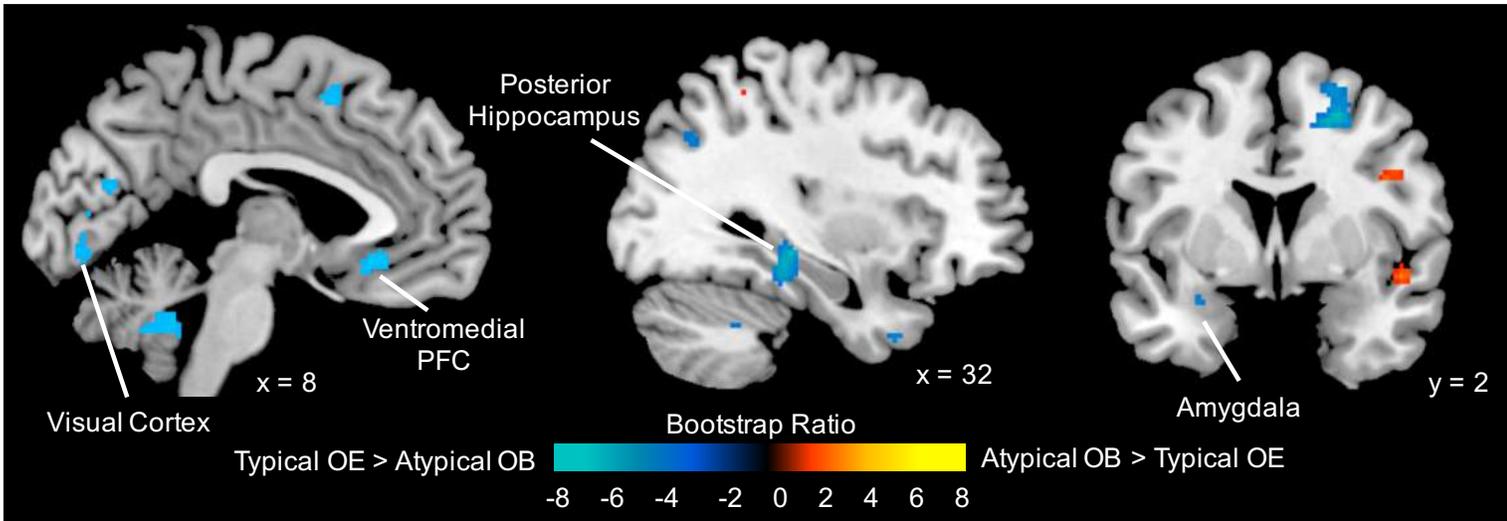


Figure 13. Hippocampus Functional Connectivity During Elaboration. The pattern of functional connectivity with the left anterior hippocampus identified in LV2 showing differences between typical OE and atypical OB conditions during elaboration (i.e., time lags 2 to 6; time lag 3 shown here). All images depict a BSR threshold of ± 3 .

The seed PLS analysis also identified a fourth significant LV that reflected differences between both OB conditions and the typical spatial condition (see Table 8). During early retrieval (i.e., time lags 1 to 2), the typical spatial condition was associated with greater functional connectivity between the hippocampus and a distributed set of cortical regions, including bilateral precuneus, prefrontal, and parietal cortices and right supplementary motor area. Substantial differences in hippocampal functional connectivity favoring the OB conditions did not manifest until time lag 3 and primarily implicated lateral temporal cortices. However, as

| | | | | | | | | | | | | | |
|------------------------------|----|-----|-----|-------|-------|---------------------------|----------------------------------|-----|-----|-----|-------|-------|-----|
| Visual Cortex | 19 | -36 | -82 | -14 | 4.92 | 308 | Middle Cingulate Cortex | 31 | 6 | -32 | 50 | -4.49 | 149 |
| | 19 | 54 | -66 | 16 | 3.45 | 26 | Somatosensory Cortex | 5 | 16 | -20 | 50 | -5.55 | 56 |
| | 18 | 34 | -92 | 6 | 5.51 | 249 | | 1 | 42 | -32 | 64 | -4.44 | 50 |
| Negative Correlations | | | | | | | Inferior Parietal Cortex | 40 | -40 | -36 | 10 | -4.66 | 131 |
| Lateral Frontopolar Cortex | 10 | 20 | 60 | -2 | -3.89 | 36 | Fusiform Cortex | 37 | 44 | -46 | -2 | -4.36 | 44 |
| Ventrolateral PFC | 47 | -28 | 32 | -12 | -3.77 | 35 | Visual Cortex | 19 | -16 | -68 | -4 | -3.47 | 50 |
| | 45 | 42 | 30 | 8 | -3.67 | 28 | | 19 | 24 | -76 | 26 | -3.75 | 34 |
| Anterior Premotor Cortex | 8 | 30 | 26 | 58 | -5.11 | 29 | | 19 | -20 | -40 | -2 | -4.75 | 25 |
| Premotor Cortex | 6 | -16 | -18 | 44 | -6.28 | 109 | | 19 | 14 | -88 | 24 | -3.41 | 22 |
| | 6 | 14 | -8 | 62 | -5.50 | 63 | Pons | | 12 | -24 | -28 | -4.11 | 50 |
| | 6 | 20 | -16 | 66 | -4.48 | 40 | Crus II Lobule of the Cerebellum | 38 | -38 | -38 | -4.08 | 32 | |
| Motor Cortex | 4 | 36 | -26 | 48 | -5.01 | 125 | Cerebellum Lobule IV, V | 24 | -36 | -30 | -5.10 | 64 | |
| Anterior Cingulate Cortex | 24 | -8 | 12 | 28 | -4.56 | 28 | | 14 | -40 | -16 | -3.99 | 36 | |
| Hippocampus | | -22 | -6 | -22 | -6.07 | 161 | | | | | | | |
| Entorhinal Cortex | 36 | -36 | -10 | -28 | -3.99 | 29 | | | | | | | |
| | 36 | -28 | -22 | -20 | -3.69 | 22 | Time Lag 6 | | | | | | |
| Insula | 13 | -36 | -14 | 8 | -4.40 | 43 | Positive Correlation | | | | | | |
| Superior Temporal Cortex | 22 | 42 | -4 | -20 | -7.10 | 464 | Visual Association Cortex | 18 | 24 | -86 | -4 | 3.67 | 22 |
| | 38 | 50 | 14 | -24 | -4.38 | 93 | Negative Correlations | | | | | | |
| Middle Temporal Cortex | 21 | -52 | -22 | -18 | -4.57 | 32 | Ventrolateral PFC | 45 | 40 | 30 | 4 | -3.89 | 84 |
| Somatosensory Cortex | 5 | 6 | -36 | 52 | -3.80 | 44 | | 47 | -26 | 32 | -10 | -4.02 | 31 |
| | 1 | 36 | -34 | 68 | -4.16 | 30 | | 47 | 58 | 34 | -10 | -3.76 | 22 |
| | 1 | -6 | -34 | 64 | -4.00 | 25 | Anterior Premotor Cortex | 8 | -8 | 32 | 42 | -4.74 | 85 |
| Inferior Parietal Cortex | 40 | 66 | -8 | 32 | -6.29 | 34 | Premotor Cortex | 6 | -14 | -18 | 44 | -5.17 | 92 |
| Visual Cortex | 19 | -28 | -52 | -2 | -3.92 | 28 | | 6 | -46 | -4 | 26 | -5.54 | 67 |
| | 18 | -18 | -70 | -2 | -4.84 | 63 | | 6 | 14 | -8 | 58 | -5.68 | 50 |
| Caudate | 20 | 0 | 16 | -4.05 | 44 | | 6 | 48 | -4 | 50 | -4.22 | 34 | |
| Pallidum | 22 | 0 | -8 | -4.73 | 66 | | 4 | -42 | -16 | 44 | -4.10 | 29 | |
| Putamen | 28 | 10 | 4 | -5.29 | 53 | Motor Cortex | 32 | -2 | 26 | 34 | -3.70 | 23 | |
| Thalamus | 10 | -18 | 0 | -5.17 | 49 | Anterior Cingulate Cortex | | 32 | -2 | -24 | -6.10 | 137 | |
| Pons | -4 | -18 | -24 | -4.11 | 54 | Amygdala | | | -24 | -8 | -20 | -6.75 | 173 |
| Cerebellum Lobule III | -8 | -42 | -18 | -4.35 | 51 | Hippocampus | | | | | | | |
| Cerebellum Lobule IV, V | 12 | -42 | -16 | -4.55 | 33 | Insula | 13 | -38 | 14 | -6 | -5.11 | 62 | |
| Vermis | -2 | -66 | -26 | -3.62 | 32 | | 13 | 32 | -14 | 20 | -4.45 | 21 | |
| | | | | | | | 41 | -40 | -38 | 10 | -4.71 | 30 | |
| | | | | | | | 38 | 28 | 10 | -40 | -4.79 | 163 | |
| | | | | | | | 22 | 56 | -6 | -14 | -4.71 | 92 | |
| | | | | | | | 38 | -38 | 2 | -40 | -4.36 | 46 | |
| | | | | | | | 38 | 56 | 18 | -22 | -3.67 | 23 | |
| | | | | | | | 22 | -52 | 6 | -4 | -4.07 | 23 | |
| Positive Correlations | | | | | | | 1 | -2 | -36 | 64 | -4.15 | 163 | |
| Posterior Cingulate Cortex | 31 | 22 | -50 | 30 | 4.45 | 22 | Somatosensory Cortex | 1 | 64 | -8 | 38 | -5.41 | 85 |
| Visual Association Cortex | 18 | -26 | -90 | -14 | 4.36 | 195 | | 5 | 22 | -30 | 48 | -6.18 | 78 |
| | 18 | 34 | -94 | 6 | 4.46 | 191 | Superior Parietal Cortex | 7 | 20 | -46 | 46 | -5.35 | 24 |
| Negative Correlations | | | | | | | Visual Cortex | 18 | 0 | -88 | -4 | -4.15 | 185 |
| Ventrolateral PFC | 45 | 48 | 34 | 0 | -4.15 | 98 | | 19 | -28 | -90 | 26 | -3.88 | 102 |
| | 47 | -26 | 30 | -10 | -4.73 | 72 | | 19 | 20 | -86 | 42 | -4.04 | 71 |
| | 44 | -42 | 12 | 6 | -5.85 | 34 | | 18 | 12 | -86 | 20 | -4.00 | 54 |
| Anterior Premotor Cortex | 8 | 4 | 24 | 34 | -4.22 | 34 | | 19 | -12 | -88 | 42 | -4.09 | 52 |
| | 8 | 32 | 26 | 58 | -3.86 | 23 | Thalamus | | 6 | -8 | 0 | -4.39 | 41 |
| Premotor Cortex | 6 | -16 | -18 | 44 | -6.66 | 107 | Pons | 4 | -20 | -30 | -4.94 | 168 | |
| | 6 | 18 | -16 | 64 | -4.16 | 36 | Cerebellum Lobule III | -4 | -42 | -20 | -4.54 | 92 | |
| | 6 | 6 | -18 | 68 | -3.72 | 31 | Cerebellum Lobule IV, V | -12 | -54 | -18 | -4.86 | 37 | |
| | 6 | 46 | -2 | 58 | -4.13 | 24 | | 22 | -44 | -32 | -4.63 | 115 | |
| Motor Cortex | 4 | 50 | -16 | 52 | -5.35 | 82 | Vermis | 0 | -62 | -24 | -4.17 | 44 | |
| Amygdala | 53 | -24 | -6 | -20 | -7.22 | 108 | | | | | | | |
| Superior Temporal Cortex | 38 | 28 | 10 | -40 | -5.14 | 53 | | | | | | | |
| | 22 | 58 | -8 | -14 | -5.50 | 71 | | | | | | | |
| | 38 | 46 | 26 | -30 | -4.28 | 45 | | | | | | | |

PFC = Prefrontal Cortex

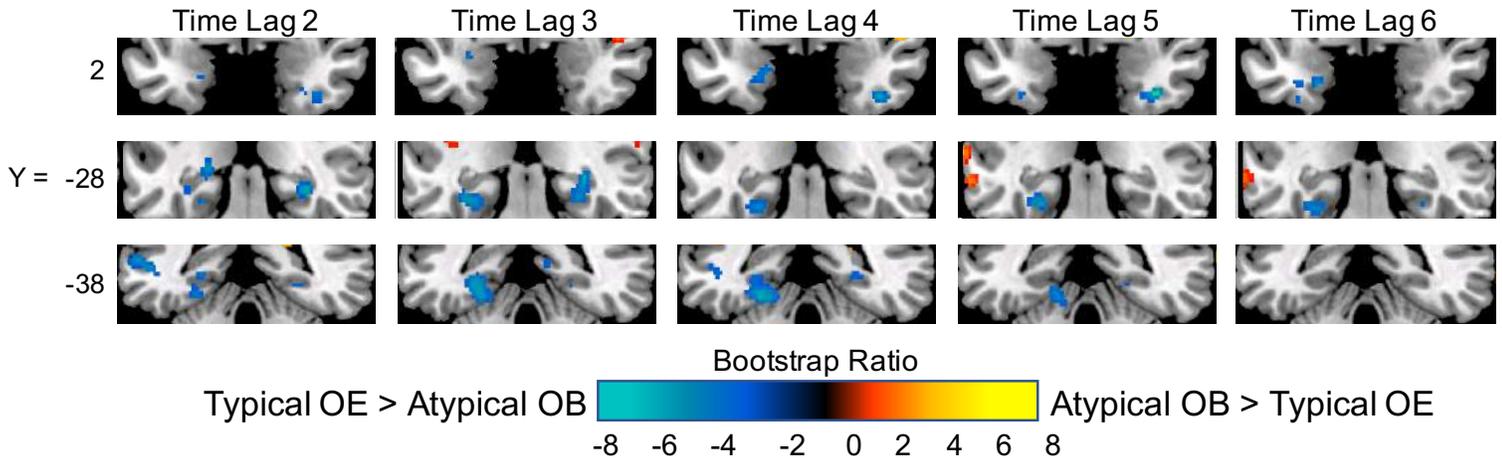


Figure 14. *Within-MTL Functional Connectivity During Elaboration LV3.* The pattern of functional connectivity with the left anterior hippocampus identified in LV3, which shows within-MTL differences in the OB versus typical Spatial conditions during elaboration (i.e., time lags 2 to 6). All images depict a BSR threshold of ± 3 .

In sum, the findings from the seed PLS analysis revealed differences throughout retrieval in the functional connectivity of the left anterior hippocampus between retrieving autobiographical memories from atypical OB versus typical OE perspectives, and retrieving autobiographical memories from both OB perspectives versus spatial visualization of the proximal aspects of a familiar location. Adoption of atypical OB perspectives involved hippocampal functional connectivity with a posterior medial network (i.e., thalamus, retrosplenial cortex, precuneus, and angular gyrus) early during retrieval, whereas adoption of typical OE perspectives involved hippocampal connectivity with an MTL network (i.e., within-MTL and ventromedial PFC) later during retrieval. Further differences between the OB and typical spatial conditions demonstrated a continuum of within-MTL connectivity whereby connectivity during later phases of retrieval was strongest in the typical OE condition, moderate in the OB conditions, and weakest in the typical spatial condition.

2.5 Discussion

Findings reveal that visual perspective is related to fundamental differences in the spatiotemporal dynamics of the brain networks that underlie autobiographical memory retrieval. Theories of memory suggest that the initial retrieval of events involves a constructive process of searching for, accessing, and assembling stored information, which is followed by the re-experiencing and elaboration of the sensory and perceptual qualities of memories (Cabeza & St. Jacques, 2007; Conway & Pleydell-Pearce, 2000). Using a multivariate analytical technique, my results provide evidence that the particular visual perspective adopted during retrieval relates to how memories are constructed and elaborated. I found that adopting a particular visual perspective is linked to differences in neural mechanisms governing the elaboration of autobiographical memories, as reflected by increased neural recruitment of a core autobiographical memory retrieval network (i.e., MTL, anterior and posterior midline regions, lateral PFC and posterior parietal cortices) for OE compared to OB perspectives. Further, behavioral PLS analyses revealed that these effects could not be accounted for by differences in construction reaction times or in-scan subjective ratings. However, hippocampal functional connectivity analyses revealed key differences in how visual perspective interacted with neural regions during both construction and elaboration of autobiographical memories. There was stronger hippocampal connectivity with a posterior medial network during construction of autobiographical memories from atypical OB perspectives, but stronger connectivity with an MTL network during elaboration of autobiographical memories from typical OE perspectives. Taken

together, these results demonstrate that visual perspective is closely connected to how and when different neocortical systems guide memory retrieval. The present findings imply a need to consider the particular visual perspective adopted during retrieval in future studies on the neural basis of autobiographical memory, which has often been ignored by previous investigations.

Only a handful of functional neuroimaging studies have investigated how visual perspective influences autobiographical memory retrieval (Eich et al., 2009; Freton et al., 2014; Grol et al., 2017; Hebscher et al., 2018; St. Jacques et al., 2018; St. Jacques et al., 2017; St. Jacques et al., 2013). For example, Eich and colleagues (2009) found greater recruitment of the amygdala for OE perspectives coupled with reduced neural recruitment of somato-motor and insular cortices for OB perspectives, which they suggested reflected reductions in emotion and embodiment when adopting an OB perspective during retrieval. In contrast, Grol and colleagues (2017) found greater recruitment of precuneus and temporoparietal junction for OB compared to OE perspectives, which they linked to increased involvement of self-referential and visuospatial processing for OB perspectives. In the current study we did not find regions reported in previous investigations on the neural representation of visual perspective in autobiographical memory that contributed more for OE compared to OB perspectives, or vice versa. However, there are several methodological differences between the current study and past research that could explain these different results. For example, Eich and colleagues (2009) used complex lab-based events based on physical actions that may have depended more on somato-motor and insular cortices when compared

with the AMs used in the present study, which varied in content and type of event retrieved. Additionally, here I directly elicited autobiographical memories associated with OE and OB perspectives, which may have reduced demands to shift to an alternative visual perspectives supported by the precuneus (e.g., St. Jacques et al., 2018; 2017). Instead, the present findings suggest that visual perspective is associated with how particular brain regions interact with the hippocampus across both construction and elaboration phases of AM retrieval, related to changes in neural recruitment in a core memory retrieval network.

Visual perspective was related to alterations in hippocampal functional connectivity during both the construction and elaboration phases of AM retrieval. The hippocampus is crucial for binding together disparate elements of memories that support mental constructions and contribute to vivid recall (for recent reviews see Palombo, Keane, & Verfaellie, 2015; Maguire, Intraub, & Mullally, 2016; Robin, 2018; Sheldon & Levine, 2016). During memory retrieval the hippocampus acts as a hub to coordinate the spatiotemporal dynamics of construction and elaboration (McCormick et al., 2015) and the timing of multiple large-scale brain networks (e.g., Inman, James, Vytal, & Hamann, 2018; St. Jacques et al., 2011). Additionally, previous research has demonstrated that the hippocampus is recruited during memory retrieval from both OE and OB perspectives (Eich et al., 2009; Grol et al., 2017; St. Jacques et al., 2018; 2017), except when memories are formed from OB perspectives (Bergouignan et al., 2014). Here, we focused on a seed region placed in the anterior portion of the hippocampus that was engaged during autobiographical memory retrieval from both OE and OB perspectives. Recent

theories have postulated functional specialization along the long axis of the hippocampus, with anterior portions supporting the flexible construction of mental scenarios and more posterior portions supporting the detailed retrieval of local aspects of an event (for reviews see Addis & Schacter, 2012; Moscovitch, Cabeza, Winocur, & Nadel, 2016; Poppenk, Evensmoen, Mocoovitch, & Nadel., 2013; Schlichting & Preston, 2015; Zeidman & Maguire, 2016). The present study's findings demonstrate that OE and OB perspectives are differentially related to the pattern of co-activation with the anterior hippocampus, suggesting that an important factor underlying the transient connectivity supporting autobiographical memory (e.g., McCormick et al., 2015) is the particular visual perspective adopted during retrieval.

In the present study, visual perspective was associated with differential patterns of hippocampal-neocortical interactions as a specific autobiographical memory was searched for and selected, thereby biasing how spatial and contextual information is reconstructed early during retrieval. During the initial construction of autobiographical memories from atypical OB compared to OE perspectives there was greater integration between the hippocampus and a posterior medial network that included thalamus, posterior parahippocampal cortex, retrosplenial cortex, precuneus and angular gyrus. The posterior medial network is thought to support the construction of situational models of events by assembling spatial and temporal contextual information from a particular egocentric perspective (Ranganath & Ritchey, 2012), which contributes to the recollection of memories as well as related processes of scene construction and imagination of

hypothetical events (Robin, 2018). Computational theories of memory and imagery additionally specify that interactions between the hippocampus and posterior medial network enable stored allocentric memory representations to be transformed to egocentric ones during long-term memory retrieval (Byrne et al., 2007). My findings reveal that the particular egocentric perspective adopted when constructing events modulates how and when the posterior medial network interacts with the hippocampus. Atypical (i.e., floor-level) but not typical (i.e., eye-level) OB perspectives were supported by greater hippocampal integration with the posterior medial network when compared to typical OE perspectives. One reason may be that adopting an atypical OB perspective required greater translation between allocentric and egocentric representations in memory and placed greater demands on the transformation circuit (e.g., Dhindsa et al., 2014; Lambrey, Doeller, Berthoz, & Burgess, 2012), consistent with evidence that actively shifting from a dominant to an alternative visual perspective during autobiographical memory retrieval involves greater recruitment of precuneus and angular gyrus (St. Jacques et al., 2017). These findings highlight the need to better understand the variety of visual perspectives that can be taken during memory retrieval (e.g., Rice & Rubin, 2011), in line with research demonstrating that multiple visual perspectives can be flexibly adopted during conscious experience and impact how memories are formed and later retrieved (Bergouignan et al., 2014).

As autobiographical memory retrieval progressed there was a reversal in the pattern of hippocampal-precuneus functional connectivity favouring OE compared to OB perspectives. The precuneus has been linked to elaboration of

autobiographical memories (Daselaar et al., 2008), in line with theories of autobiographical memory that postulate that perceptual and visual imagery processes occur later during retrieval (e.g., Conway & Pleydell-Pearce, 2000) and the role of precuneus in egocentric mental imagery (Cavanna & Trimble, 2006). However, present findings suggest that functional connectivity between the hippocampus and precuneus emerges much earlier during the time-course of autobiographical memory retrieval depending upon the particular visual perspective adopted. Recent evidence links the precuneus to mental orientation processes that determine relationships between an individual and their surroundings in terms of space, people, and time (Peer, Salomon, Goldberg, Blanke, & Arzy, 2015). Thus, one intriguing interpretation of the current findings is that OB perspectives place early demands on mental orientation processes because they require greater spatial transformation to instantiate a non-dominant perspective. In contrast, OE perspectives may require mental orientation processes only after perceptual and sensory information is recovered.

During late retrieval, adoption of typical OE compared to atypical OB perspectives was also supported by greater integration within an MTL network that included ventromedial PFC, amygdala, posterior parahippocampal, hippocampal, entorhinal, and visual cortices, suggesting that typical OE perspectives are better able to access declarative memory processes under the purview of the MTL network. In support of the role of the MTL network in the retrieval of specific events, a similar pattern of within-MTL connectivity also contributed more to autobiographical memories retrieved from both typical and atypical OB

perspectives when compared to spatial visualization of proximal aspects of a familiar location, which by nature involve less emphasis on episodic memory processes. Similarly, St. Jacques and colleagues (2013a) showed greater integration in an MTL network centered on the hippocampus among people who spontaneously recalled more AMs from stronger OE perspectives. Here I replicate these findings but also significantly extend them by demonstrating that people can flexibly engage this network in the service of retrieving memories from a specific perspective. The MTL network is implicated in the retrieval of episodic information contributing to the recollection or visualization of mental scenes and hypothetical events (Andrews-Hanna et al., 2010; Benoit & Schacter, 2015; Kahn, Andrews-Hanna, Vincent, Snyder, & Buckner, 2008; Madore, Szpunar, Addis, & Schacter., 2016; St. Jacques et al., 2011). In particular, amygdalar-hippocampal interactions are thought to contribute to the recollection of memories based on salient item-specific details, which may be further supported by the recapitulation of perceptual information in the ventral visual stream via projections to the hippocampus from the entorhinal cortex (for review see Buchanan, 2007; Phelps & Sharot, 2008; Yonelinas & Ritchey, 2015).

Autobiographical memory retrieval from a typical OE compared to atypical OB perspective also resulted in co-activation of the anterior hippocampus and ventromedial PFC. Ventromedial PFC is a member of the MTL-network linked to conceptual aspects of self-reference and affective value (e.g., Bergström, Vogelsang, Benoit, & Simons, 2015; Lin, Horner, & Burgess., 2016) that enable the formation of abstract mental models or schemas about the world and oneself in

order to extract meaning to guide behavior (for reviews see D'Argembeau, 2013; Gilboa & Marlatte, 2017; Morton, Sherrill, & Preston, 2017; Robin & Moscovitch, 2017; Roy, Shohamy, & Wager, 2012). During retrieval, interactions between the ventromedial PFC and the anterior hippocampus are thought to contribute to updating of reactivated memories guided by abstract memory representations or schemas (Schlichting & Preston, 2015), which may contribute to the transformation of memories overtime (Moscovitch et al., 2016). Present results suggest that autobiographical memories retrieved from an OE perspective tend to rely more heavily on schematic information, as indexed by increased hippocampal connectivity with ventromedial PFC (Robin & Moscovitch, 2017). In contrast, late phases of retrieval from atypical OB perspectives was associated with increased hippocampal connectivity with dorsomedial PFC, which is linked to the processing of social information related to other people (for metaanalysis see Denny, Kober, Wager, & Ochsner, 2012). For example, St. Jacques, Conway, Lowder, & Cabeza (2011) found that dorsomedial PFC is recruited to a greater extent when people were asked to understand another person's perspective, whereas ventromedial PFC was recruited more during autobiographical memory retrieval for events cued from an OE perspective (also see Rabin, Gilboa, Stuss, Mar, & Rosenbaum, 2010). The ventral versus dorsal distinction in the medial PFC found here could reflect differences in how autobiographical retrieval from OE and OB perspectives are guided by self-related schemas (e.g., Libby & Eibach, 2011; Sutin & Robins, 2008). Moreover, the ability to adopt multiple egocentric perspectives that vary in their self-distance in memories offers a potential bridge between self- and other-related

representations that enable us to understand mental states in others (de la Vega, Chang, Banich, Wager, & Yarkoni, 2016).

Visual perspective was also related to neural recruitment in a core autobiographical memory retrieval network during late retrieval in a similar way to other aspects of mental imagery that tend to occur during the elaboration of autobiographical memories (e.g., Conway, Pleydell-Pearce et al., 2001; Daselaar et al., 2008), and perhaps due to changes in the functional integration with the hippocampus (e.g., McCormick et al., 2015). Specifically, OE perspectives recruited the autobiographical memory retrieval network to a greater extent compared to OB perspective, demonstrating that OE perspectives involve increased access to memory details as they are elaborated. This finding is consistent with our hippocampal functional connectivity results revealing increased connectivity with an extended MTL-network for OE relative to atypical OB perspectives during late stages of retrieval. Critically, the pattern of neural recruitment during elaboration of autobiographical memories from multiple visual perspectives was also distinguished from general differences in visualizing a scene from alternative viewpoints.

Moreover, this pattern was not directly related to behavioural differences in the subjective experience associated with retrieval, because there was little overlap between neural regions that contributed to behavior and those that distinguished OE and OB perspectives. The lack of overlap between regions sensitive to both phenomenological aspects of retrieval and differences in visual perspective was unexpected given that several behavioural studies have demonstrated that visual

perspective alters phenomenology during retrieval (e.g., Berntsen & Rubin, 2006; Robinson & Swanson, 1993; Sutin & Robins, 2009), which are thought to contribute to differences in neural recruitment as has sometimes been reported (e.g., Eich et al., 2009; Grol et al., 2017). In the current study, the slower construction times for autobiographical memories experienced from typical OB perspectives also shortened the subsequent elaboration period and may have obscured the association between visual perspective and subjective aspects of elaboration (i.e., vividness and emotional intensity). However, our findings also point to the differences in hippocampal interactions with the posterior medial network and a wider MTL network, which could have contributed to subjective changes in autobiographical memory retrieval due to visual perspective.

Conclusion. Egocentric perspective is a defining feature of memories for events (Bryne et al., 2007; Robins, 2018; Rubin & Umanath, 2015), but this self-centered aspect of remembering has been elusive to investigation due to its ubiquitous nature (Prebble, Addis, & Tippett, 2013). Here, by manipulating multiple visual perspectives during autobiographical memory retrieval, we demonstrate for the first time how egocentric perspective is related to the neural mechanisms that contribute to the time-course of autobiographical memory retrieval. We found that OE and OB perspectives were associated with identical patterns of activation in the autobiographical memory retrieval network during elaboration, but to a lesser extent for OB perspectives, revealing increased processing of memory details for OE perspectives. However, functional connectivity with the hippocampus revealed earlier posterior medial network involvement when adopting an atypical OB

perspective, highlighting reconstructive spatial transformation processes required to instantiate alternative viewpoints in a mental scene. We also observed greater hippocampal connectivity with an MTL network when adopting a typical OE perspective during elaboration, further suggesting that OE perspectives are better able to access episodic memory processes during the elaboration of specific event details. The current findings contribute to research on how visual perspective shapes memories during retrieval (e.g., Marcotti and St. Jacques, 2018; St. Jacques et al., 2017) and imply a need for future neuroimaging studies of autobiographical memory to account for this core aspect of retrieval. Better understanding of the neural mechanisms that support the fundamental capacity to understand ourselves from multiple perspectives when remembering the past could also contribute to research on how we flexibly understand the perspective of others (Carrington & Bailey 2009).

**Chapter 3: Neural Mechanisms Underlying Visual Perspective and Bodily
Selfhood in Memories for Events**

3.1 Abstract

While memory encoding is often assumed to only occur from an in-body perspective (i.e., first-person perspective), out-of-body experiences demonstrate that we also have the capacity to step outside of ourselves and form memories from a third-person perspective (e.g. Blanke, Landis, Spinelli, & Seeck, 2004; Nigro & Neisser, 1983). This phenomenon offers a unique opportunity to investigate how bodily selfhood interacts with visual perspective during memory encoding to shape the way in which a past event is recalled. Yet, little is known of the neural mechanisms that support the combined influence of visual perspective and sense of bodily self in memory. Here, participants formed memories for a series of realistic events following an illusion induction that manipulated their sense of bodily self from in-body and out-of-body perspectives. Memories for these events were recalled during functional scanning later that day, and representational similarity analysis was conducted to examine how patterns of activity within the brain reflected visual perspective and sense of bodily self during retrieval. I found that posterior cingulate cortex was able to differentiate between memories encoded from different visual perspectives. Further, patterns of activity within both posterior cingulate cortex and the angular gyrus represented the interaction between visual perspective and bodily selfhood along a continuum ranging from an embodied, in-body perspective to a disembodied, out-of-body perspective. Together, these results help to elucidate how fundamental aspects of selfhood, namely the feeling of being located within and experiencing the world from the perspective of one's own body, are integrated within memory.

3.2 Introduction

Memory retrieval requires adopting a particular visual perspective within a mental scene, which can either be centred within the body, affording a first-person perspective, or outside of the body, whereby one is able to see oneself in a memory from a third-person perspective (Nigro & Neisser, 1983). Yet, little is known about the neural mechanisms that support this indispensable component of memories (Rubin & Umanath, 2015). The handful of neuroimaging studies that have investigated the role of visual perspective in memory have focused on retrieval processes (Eich, Nelson, Leghari & Handy, 2009; Freton et al., 2014; Grol, Vingerhoets, & De Raedt, 2017; Hebscher, Levine, & Gilboa, 2018; St. Jacques, Carpenter, Szupunar, & Schacter, 2017; St. Jacques, Szupunar, & Schacter, 2017). However, even less is known about how visual perspective at encoding influences memories for past events (Bergouignan et al., 2014). An important factor in evaluating the influence of visual perspective on memory encoding is bodily self-consciousness, comprised of bodily ownership, self-location, and experiencing the world from perspective within the body (Blanke, 2012). Previous research on memories encoded from an in-body perspective has shown that retrieval from an in-body perspective results in a heightened focus on physical sensations and the emotional reactions they trigger (Bagri & Jones, 2009; Bernstein & Rubin, 2006; Mclsaac & Eich, 2002). In contrast, retrieval of events encoded from an in-body perspective from an out-of-body perspective necessarily involves a dissociation from one's body, allowing it to be perceived from a third-person perspective. Yet, how bodily self-consciousness interacts with visual perspective at

encoding to influence neural mechanisms underlying memory retrieval has only been considered by one other investigation (Bergouignan, Nyberg, & Ehrsson, 2014). Here, I manipulated visual perspective and sense of embodiment during memory formation, and used representational similarity analysis (Kriegeskorte, Mur, & Bandettini, 2008) to investigate how these fundamental aspects of selfhood are reflected by multivariate patterns of neural activity during retrieval.

Embodiment is typically manipulated experimentally by capitalizing on the multisensory nature of brain mechanisms that determine bodily self-consciousness (e.g. Petkova & Ehrsson, 2008; Van Der Hoort, Guterstam & Ehrsson, 2011; Guterstam, Björnsdotter, Gentile, & Ehrsson, 2015). In these experiments, participants are asked to wear a virtual reality head-mounted display (HMD) unit linked to a camera mounted on a mannequin, allowing the participant to see the lab from its point of view. Next, the experimenter applies brushstrokes to the mannequin and corresponding locations on the participant's physical body. When brushstrokes are applied synchronously, the combination of congruent visual and tactile information leads participants to feel an illusory sense of embodiment over the mannequin's body. However, feelings of bodily selfhood are not affected when brushstrokes are applied asynchronously, due to a mismatch between incoming visual and tactile signals. Strength of these full-body illusions is assessed using questionnaires and physiological recordings, such as skin conductance responses (e.g. Saloman et al., 2013; Guterstam & Ehrsson, 2012). Recently this paradigm has been used to establish ownership over an invisible body, demonstrating the incredibly plastic underpinnings of bodily selfhood (Guterstam, Abdulkarim, &

Ehrsson, 2015). Participants wore HMD units mounted to a wall such that they could see empty space below the cameras. The experimenter applied synchronous brushstrokes to the participant's torso and limbs and corresponding locations in empty space within the field of view of the camera, causing an illusory sense of embodiment within an invisible body located directly beneath the camera. The invisible body illusion did not occur following asynchronous visuotactile stimulation. However, in this study participants' physical bodies were not visible in their field of view during the illusion induction. In the present study, I used the invisible body illusion to manipulate sense of bodily selfhood from in-body and out-of-body perspectives that include participants' bodies in their field of view, mimicking clinical reports of out-of-body experiences defined by perceiving oneself from a third-person perspective (Blanke, Landis, Spinelli, & Seeck, 2004).

Previous research suggests that visual perspective and sense of bodily self may be supported by activity within medial temporal lobe (MTL) and posterior parietal regions. Within the MTL, the hippocampus and parahippocampus have been shown to contain information conveying an individual's sense of self-location during full-body illusions (Guterstam, Bjornsdotter, Gentile, & Ehrsson, 2015; Guterstam et al., 2015c), which may contribute to how memories are encoded and later retrieved. Consistent with this idea, repetition enhancement effects have been reported in response to repeatedly retrieving memories encoded from an out-of-body perspective in the left posterior hippocampus, which were correlated with reductions in vividness and coincided with impaired recall of episodic details (Bergouignan et al., 2014). In contrast, memories encoded from an in-body

perspective were linked to repetition suppression effects over repeated trials within the hippocampus. This initial study suggests that forming memories from an out-of-body perspective disrupts encoding mechanisms in the hippocampus, which alters later activation during retrieval. The parahippocampal cortex may also be sensitive to changes in visual perspective, based on evidence implicating this region in processing the spatial layout of scenes (Epstein, Harris, Stanley, & Kanwisher, 1999; Epstein & Kanwisher, 1998), in a viewpoint dependent manner (Epstein, Graham, & Downing, 2003). For example, Epstein and colleagues presented participants with two photos of objects upon a table that differed according to the viewing angle from which the photo was taken or spatial relationships among objects during functional scanning. They found that posterior parahippocampal cortex responded with equal strength to changes in viewing angle and spatial relationships among objects. These results indicate that the posterior parahippocampus is involved in processing the spatial configuration of scenes depending upon the vantage point from which a scene is viewed (Aminoff et al., 2014; Epstein et al., 2003), which suggests that this region may be sensitive to differences in egocentric perspective during memory formation. Thus, existing evidence implicates the hippocampus and parahippocampus in establishing a sense of self-location during perception (Guterstam et al., 2015b; Guterstam et al., 2015c), and retrieving mental scenes dependent on visual perspective (Bergouignan et al., 2014) and viewing angle (Epstein et al., 2003) respectively. Together, these findings suggest that the hippocampus and parahippocampus may be sensitive to the combined influence of visual perspective and embodiment when

retrieving events encoded from different perspectives to support spatial memory processes.

Outside the MTL, posterior cingulate cortex may also contain an integrated representation of visual perspective and sense of bodily self. Like the hippocampus and parahippocampus, patterns of activity within posterior cingulate cortex convey an individual's sense of self-location (Guterstam and colleagues, 2015b). However, unlike MTL regions, the posterior cingulate cortex integrates self-location with feelings of bodily ownership to enable a merged sense of bodily self (Guterstam and colleagues, 2015b). A coherent sense of bodily selfhood may then be incorporated into memories within posterior cingulate cortex, as this region is known to be active during successful memory retrieval (Rugg & Vilberg, 2014) and self-referential processing (Andrews-Hanna et al., 2010; Leech & Sharp, 2013). However, Guterstam and colleagues (2015b) did not address how experiencing the world from an in-body perspective, a key component of bodily self-consciousness (Blanke, 2012), may be integrated with the two other aspects of bodily self-consciousness related to self-location and bodily ownership. Thus, the present study will elucidate how visual perspective, bodily ownership, and self-location are processed within posterior cingulate cortex, ultimately contributing to an integrated sense of the bodily self within memories.

Bodily selfhood may then be integrated with additional multimodal memory features within a common egocentric perspective in the angular gyrus (Bonnici et al., 2018; Bonnici et al., 2016; Yazar et al., 2017), which can in turn be manipulated in the precuneus during memory retrieval (St. Jacques, Carpenter, Szupunar, &

Schacter, 2018; St. Jacques, Szupunar, & Schacter, 2017). For example, disrupting activity in the angular gyrus through brain damage (Ionta et al., 2011), seizures (Blanke et al., 2004), or transcranial magnetic stimulation (Blanke, Ortigue, Landis, & Seeck, 2002) leads to out-of-body experiences. Further lesions in the angular gyrus are associated with reduced use of in-body perspective imagery during mental navigation (Ciaramelli et al., 2010). Neuropsychological evidence is supported by the finding that continuous theta burst stimulation to the left angular gyrus reduces the tendency to retrieve memories from an in-body perspective (Bonnici et al., 2018). However, the angular gyrus may be implicated in instantiating both types of visual perspectives. Recently, St. Jacques, Szupunar, and Schacter (2017) found that shifting between visual perspectives was associated with increased activity in the right angular gyrus, which suggests that this region is involved in representing both in-body and out-of-body perspectives. Additionally, Grol, De Raedt, and Vingerhoets (2017) reported increased activity in this region in response to retrieving memories from an out-of-body compared to in-body perspective, which the authors attributed to mental transformation processes required to update visual perspective (Grol, De Raedt and colleagues, 2017). Thus, further research is required to elucidate the role of this region in establishing egocentric frameworks during memory retrieval. Once an egocentric perspective is established in the angular gyrus, it can be manipulated in the precuneus. Both St. Jacques and colleagues (2017) and Grol and colleagues (2017) found that adopting to a novel visual perspective activated the precuneus, which has previously been associated with visual mental imagery (Cavanna & Trimble, 2006;

Fletcher et al., 1995) and storage of egocentric spatial representations of an environment (Byrne, Becker, Burgess, 2007). However, structural neuroimaging studies have found that gray matter volume in the precuneus is positively related to the tendency to retrieve events from an in-body perspective (Grol et al., 2017; Hebscher et al., 2018). Conflicting results regarding the precuneus in studies of visual perspective during memory retrieval highlight a need to clarify how different visual perspectives are represented in this region.

Thus, I conducted this study in order to develop understanding of how visual perspective and sense of embodiment interact to shape patterns of activity within the hippocampus, parahippocampus, posterior cingulate cortex, angular gyrus, and precuneus during memory retrieval. Participants formed memories for a series of realistic events following an illusion induction that manipulated their sense of bodily self from in-body and out-of-body perspectives. Memories for these events were recalled during functional scanning later that day, and representational similarity analysis (Kriegeskorte et al., 2008) was conducted to examine how patterns of activity within the five selected regions of interest reflected visual perspective and sense of bodily self during retrieval. I predicted that the hippocampus, parahippocampal cortex, posterior cingulate cortex, and angular gyrus would be sensitive to the interaction between visual perspective and bodily selfhood, such that patterns of activity within these regions would be correlated with a linear relationship among conditions ranging from strongly in-body (i.e., in-body, synchronous visuotactile stimulation) to strongly out-of-body (i.e., out-of-body, asynchronous visuotactile stimulation). This prediction is based on previous

research linking activity in these regions to the domains of visual perspective and embodiment. I also predicted that patterns of activity within the hippocampus would differentiate between in-body and out-of-body perspectives, as this region has often been implicated in studies of visual perspective.

3.3 Methods

3.3.1 Participants

Participants included 28 healthy, right-handed young adults (age range: 18 to 29 years), with no prior history of neurological or psychiatric impairment, and who were not currently taking medication that affected mood or cognitive function. Participants provided informed written consent as approved by the School of Psychology at the University of Sussex. Several participants ($N = 11$) had difficulty keeping still in the scanner due to the large number of functional runs and were excluded from the analysis due to excessive movement (i.e., greater than 3 mm). Thus, the final neuroimaging analysis was performed on 18 participants (8 women; mean age = 21.05, $SD = 3.01$). These 11 participants were retained in the behavioral analyses.

3.3.2 Procedure

The first part of the experiment involved inducing an illusion to alter sense of bodily ownership, self-location, and embodiment. Participants viewed themselves from either an in-body or out-of-body visual perspective while receiving synchronous (sync) or asynchronous (async) visuotactile stimulation, resulting in four conditions (i.e., in-body sync, in-body async, out-of-body sync, out-of-body async). Once the first illusion had been induced, participants encoded a series of

brief, realistic events consisting of four word games played with the experimenter, and practiced vividly retrieving each. Participants then answered questions relating to (1) the bodily sensations experienced during the events, (2) details of each event to assess memory accuracy, and (3) subjective ratings of visual perspective, vividness, emotional intensity, and perceived memory accuracy. This process was repeated for the remaining three conditions. Later that day, participants repeatedly retrieved memories for each of the events during functional scanning, in addition to rating visual perspective and vividness. After scanning was complete, participants answered a different recall question from the one asked immediately following encoding for each event, and provided ratings of emotional intensity and perceived memory accuracy.

3.3.2.1 Illusion Induction. Two videos, one from an in-body perspective and one from an out-of-body perspective were recorded to be used in the illusion induction. A high definition 360-degree camera (i.e., Ricoh Theta S; Resolution: 1920 x 1080; Frame Rate: 29.97 frames per second) was mounted on a tripod, which was adjusted to each participant's eye level. Next, participants were fitted with an Oculus Rift head mounted display (HMD) unit and asked to stand on an "X" marked on the floor one metre in front of the tripod and facing a set of closed cabinets. The display of the HMD unit was blank for this initial part of the experiment and included to match the participant's appearance during the ensuing memory encoding portion of session one. Thus, the position of the camera on the tripod created an out-of-body perspective by affording a view of the participant's back body, as if s/he were standing behind her/himself. After starting video

recording, the experimenter approached the tripod and stroked empty space below the camera with a medium sized paintbrush in locations corresponding to the participant's torso, arms, and legs, as if applying brushstrokes to an invisible body positioned below the camera (Guterstam, Abdulkarim, & Ehrsson, 2015; see Figure 1A). The length of the participant's torso, arms, and legs were marked against a wall located behind the tripod to indicate starting and stopping points for each brushstroke, ensuring that brushstrokes matched the participant's specific body dimensions. Each brushstroke lasted one second with an additional one and a half seconds between brushstrokes (Guterstam, Abdulkarim, & Ehrsson, 2015). Five brushstrokes were applied to each of the five different body parts in the following order: torso, right arm, left arm, right leg, left leg. After the first video had been recorded, the camera was mounted to small, flexible tripod attached to the front of the HMD unit in order to create a video from an in-body perspective (see Figure 1B). Then, another video was recorded wherein the experimenter applied brush strokes to the participant's physical body using the same procedure as the first video. After both videos had been recorded, they were converted to a 360-degree MP4 format using the Ricoh Theta desktop application while the participant waited outside the lab. Videos were presented using Whirligig software, which allowed them to be visible both inside the HMD unit and on the desktop computer screen.



Figure 1. Videos used for the embodiment illusion were taken from an OB (A) and OE perspective (B).

Participants were then invited back into the laboratory where they were once again fitted with the HMD unit and stood on the “X” marked on the floor facing the cabinets. Participants were also instructed to look down at their body. Masking tape was placed on the underside of the HMD unit to ensure that the participants only saw what was presented on the screen without any additional light entering the display. The experimenter then played the video visible to the participant through the HMD unit and the experimenter through the desktop computer to the right of the participant. Brushstrokes were applied to the participant’s body either synchronously or asynchronously with the timing of brushstrokes in the video. Immediately after the induction of the embodiment illusion, the experimenter switched the video feed in the HMD unit to a live stream of the laboratory using a custom application implemented in Unity 5.3.0 (Hamanaka, 2016). The transition from recorded video to live stream less than five seconds.

3.3.2.2 Event Encoding. Immediately after each illusion induction, participants encoded interactive events selected to create realistic, distinct

memories that could later be retrieved during functional scanning. The experimenter first opened the cabinets in front of the participant revealing stimuli to be used in the memory encoding stage of the experiment. Participants played four brief (i.e., less than 10 seconds) and emotionally neutral word games with the experimenter; I spy, categories, sentence construction, and the truth game. For the I spy game, the experimenter provided a colour (e.g., “I spy with my little eye something that is brown”) as a cue and participants made two guesses as to the identity of the object based on objects located in the right-hand cabinet (e.g., hat, cardboard box; see Figure 2). In the categories game, the experimenter named a category (e.g., sports), prompting the participant to provide an example consistent with the category (e.g., cricket). The experimenter and participant took turns providing examples until a total of four were named. Each of the experimenter’s responses (e.g., weightlifting) was associated with a unique object (e.g., kettle bell) that was taken out of the left cabinet and held in front of the participant as it was named (see Table 1). During the sentence construction game, the participant and experimenter took two turns each verbalizing words to form a short sentence, beginning with the participant. The experimenter’s first response was associated with a unique object in the left cabinet to serve as a memory cue throughout the experiment, which was taken out of the cabinet and held in front of the participant as it was named (see Table 1). Lastly, the truth game involved the experimenter stating three consecutive statements based on a related topic, two of which were true and one of which was false (for full list of statements see Appendix B). Each statement was associated with a unique object in the left cabinet that was held in

front of the participant as it was named (see Table 1). For example, the experimenter would select a toy bat and say “a group of bats is called a bevy”, then select a toy owl and say “a group of owls is called a parliament”, then select a toy crow and say “a group of crows is called a murder” (see Figure 3). The participant next guessed which statement was the lie.

Each game was repeated using the exact same words a total of five consecutive times before beginning the next game. At the end of the last repetition, participants were instructed to close their eyes and retrieve the game from memory in as much detail as possible until the experimenter signalled them to stop after seven seconds, measured with a stopwatch. Repetitions and practiced retrieval were included to create a robust memory for each game that the participant would be able to retrieve from memory during functional scanning.



Figure 2. Experimental stimuli used for the I spy game.



Figure 3. Experimental stimuli for the truth game with the memory cue “groups”.

Table 1.

Experimental Stimuli for the I Spy Game

Memory Cue

| | |
|--------|--------------------------------|
| Blue | Watering Can, Ball |
| White | Fan, Plunger |
| Orange | Basketball, Cone, Toy Dinosaur |
| Brown | Cardboard box, Hat |

Experimental Stimuli for the Categories Game

| | |
|------------|--------------------------|
| Animals | Toy Dog, Toy Parrot |
| Vegetables | Butternut Squash, Carrot |
| Sports | Kettlebell, Bowling Pin |
| Music | Ukulele, Headphones |

Experimental Stimuli for the Sentence Construction Game

| | |
|--------|---------------|
| Plant | Potted Plant |
| Wine | Wine Bottle |
| Basket | Easter Basket |
| Clock | Wall Clock |

Experimental Stimuli for the Truth Game

| | |
|-----------|---|
| Groups | Toy Bat, Toy Owl, Toy Crow |
| Brighton | University of Sussex Sweatshirt, Photo of a Happy Face Emoji, Toy Octopus |
| Berries | Two Avocados, 5 Bananas, 1 Bowl of Strawberries |
| Favorites | Baseball Cap, Purple Gloves, Coffee Bodum |

3.3.2.3 Immediate Memory Test. After each round of four games, participants were instructed to remove the HMD unit and asked to answer a series of questions. The first of these was an out-of-body experience questionnaire (OBEQ) designed to assess bodily sensations experienced during the illusion induction and while playing the games, adapted from Guterstam, Abdulkarim, & Ehrsson (2015). It included three statements designed to assess the strength of the embodiment illusion (see Table 2, S1 to S3) and three control statements to assess a participant's susceptibility to demand characteristics (see Table 2, S4 to S6) that were rated on a 7-point Likert scale from -3 (i.e., strongly disagree) to 0 (i.e., neutral) to 3 (i.e., strongly agree). Next, participants answered one cued recall question from each game (see Appendix B), and rated their memory for each game on 7-point Likert scales according to vividness (1 = None, 7 = A Lot), emotional intensity (1 = None, 7 = A Lot), perceived accuracy (i.e., the degree to which participants felt their memory was an accurate representation of the game; 1 = A Little, 7 = Completely Accurate), and visual perspective separately for OE and OB perspectives (1 = A Little, 7 = A Lot).

Once participants had answered all questions, the next embodiment illusion was induced. This process was repeated for each of four conditions: in-body perspective with synchronous visuotactile stimulation, in-body perspective with asynchronous visuotactile stimulation, out-of-body perspective with synchronous visuotactile stimulation, out-of-body perspective with asynchronous visuotactile stimulation. Thus, participants played 4 games in each condition. The order of

conditions, games, and stimuli within each game were allocated randomly for each participant.

Table 2.

Embodiment Questionnaire Items

| | Out-of-Body Perspective | In-Body Perspective |
|----|---|---|
| S1 | I felt the touch of the brush in empty space in the location where I saw the brush moving | I felt the touch of the brush on the body I saw in the location where I saw the brush moving. |
| S2 | I experienced that the touch I felt was caused by the brush moving in the empty space. | I experienced that the touch I felt was caused by the brush touching the body I saw. |
| S3 | It felt as if I had an invisible body. | It felt as if the body I saw was my body. |
| S4 | I could no longer feel my body. | I could no longer feel my body. |
| S5 | I felt as if I had two bodies. | I felt as if I had two bodies. |
| S6 | When I saw the brush moving, I experienced the touch on my back. | When I saw the brush moving, I experienced the touch on my back. |

3.3.2.4 fMRI Scanning. Later that day (i.e., 1.5 to 3 hours following memory encoding), participants retrieved memories for each game during functional scanning. Before scanning, participants were shown the title of each memory and asked to report the associated game and stimuli to ensure they were able to recall each event using the title cue. All participants were able to recall each event. Next, participants underwent a practice session to familiarize themselves with the task and timing of responses, which involved retrieving their memory for each event once and making subjective ratings of visual perspective and vividness.

Scanning commenced after completion of the practice session. On each trial, participants were presented with the memory cue (e.g., blue) and game title (e.g., I Spy). This prompt was quickly followed (i.e., 800 ms) by an instruction to close their eyes, at which point they were asked to retrieve the memory for the event in as much detail as possible until an auditory tone sounded through MRI-compatible headphones 6.4 s later. Upon hearing the brief auditory tone,

participants were instructed to stop retrieving the event and open their eyes. They were then asked to provide subjective ratings of the degree to which they retrieved the event from an in-body perspective, the degree to which they retrieved the event from an out-of-body perspective, and how much vividness was associated with memory retrieval, each on 4-point scales from 1 = low to 4 = high. The order of the OE and OB perspective ratings was counterbalanced across participants to control for potential order effects. Participants had 2.4 s for each rating and responded using a four button MRI-compatible response box.

There were 12 functional runs consisting of 16 trials (i.e., 1 trial per event, 4 trials per condition), resulting in a total of 48 trials per condition. Trial order was randomized for each functional run. Trials were separated by a jittered fixation cross, which was equally spaced across a variable length (i.e., 1.6 to 8 s) and distributed exponentially such that shorter inter-trial intervals occurred more frequently than longer intervals.

3.3.2.5 Post-Scanning Memory Test. Immediately after scanning, participants answered a cued recall question different from the one asked immediately following memory encoding (see Appendix B), and made subjective ratings of emotional intensity and perceived memory accuracy.

3.3.3 MRI data acquisition and preprocessing.

Functional and structural images were collected on a 3T MAGNETOM Prisma MRI scanner. Detailed anatomical data were collected using a multi-planar rapidly acquired gradient echo (MPRAGE) sequence. Functional images were acquired using a T2*-weighted echo planar sequence (TR = 800 ms, TE = 37 ms,

FOV = 208 x 208 mm, Slice Thickness = 2 mm). Whole brain coverage was obtained via 72 interleaved slices, acquired at an angle corresponding to AC-PC alignment, with a multiband factor of 8 and a 2 mm x 2 mm in-plane resolution. The first ten volumes of each run were discarded to allow for T1 equilibrium.

Preprocessing of functional images was performed using SPM12 (Wellcome Department of Imaging Neuroscience, London, UK) using standard methods. Functional images were realigned within and across runs to correct for head movement, segmented into gray matter, white matter, and CSF, co-registered to the participant's anatomical image, and spatially normalized to the Montreal Neurological Institute (MNI) template. BOLD signal response patterns according to condition were estimated using a general linear model (GLM). A regressor was estimated for each condition in each of the twelve functional runs, resulting in four beta estimates per run. Regressors were time-locked to the onset of the memory cue and the duration set to cover the memory retrieval period (i.e., 6.4s), excluding the auditory tone and subjective ratings. Six movement parameters were included as separate regressors. The SPM canonical haemodynamic response basis function was used to estimate brain responses. Additionally, GLM's were estimated using the fast serial correlations option to account for the multiband sequence employed during neuroimaging data collection.

3.3.4 Definition of the ROIs.

I focused on the hippocampus, parahippocampal cortex, posterior cingulate cortex, angular gyrus and precuneus based on prior research that has linked these regions to processes related to visual perspective (e.g. Bergouignan et al., 2014;

Bonnici et al., 2018; Grol et al., 2017; Guterstam et al., 2015b). Individual bilateral masks for each region were created in WFU Pickatlas (Maldjian, Laurienti, Burdette, & Kraft, 2003) using the Individual Brain Atlases using Statistical Parametric Mapping (IBASPM; Alemán-Gómez, Melie-García, Valdés-Hernandez, 2006). Masks were then converted into binary format using the MarsBar toolbox for SPM (Brett, Anton, Valabregue, & Poline, 2002) and resampled to 2mm cubic voxels to match the dimension of the beta estimates obtained from the GLM analysis (see Figure 4).

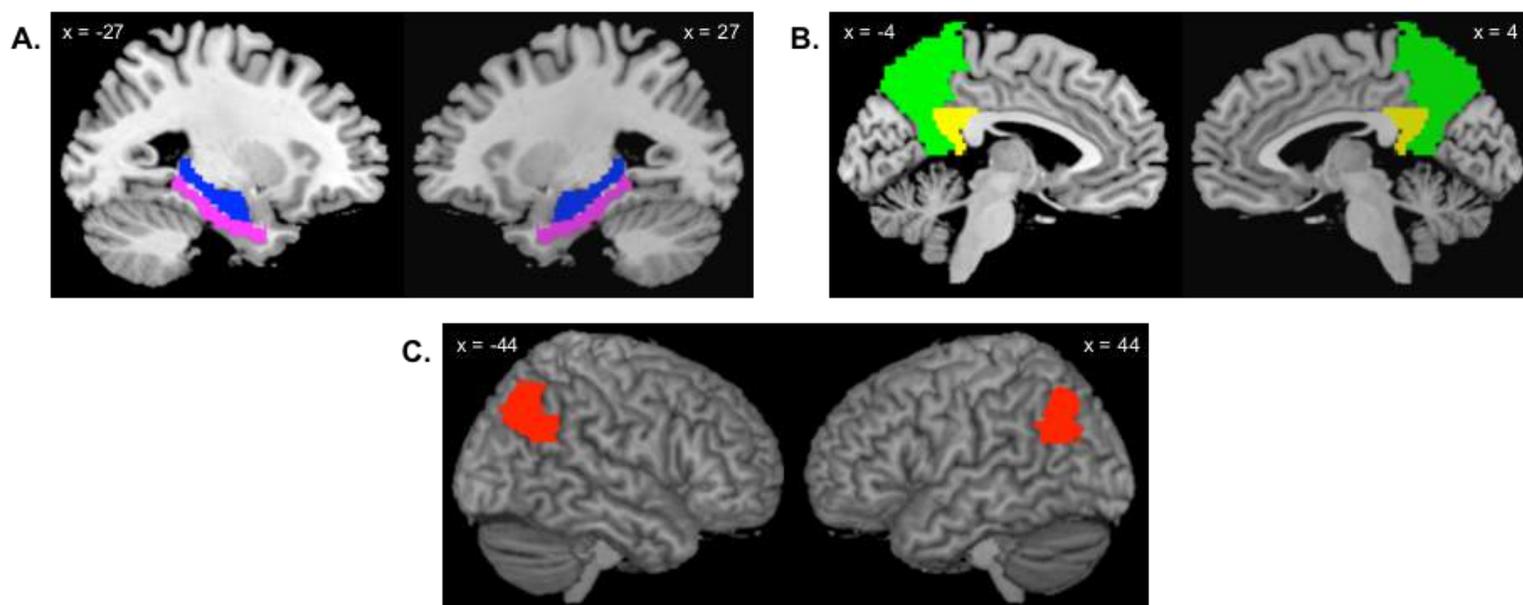


Figure 4. ROI masks of the hippocampus in pink and parahippocampus in blue (A), posterior cingulate cortex in yellow and precuneus in green (B), and angular gyrus in red (C).

3.3.5 Representational similarity analyses.

RSA was carried out in CoSMoMVPA (Oosterhof, Connolly, & Haxby, 2016). First, three target dissimilarity matrices were constructed to investigate correlations with neural dissimilarity within each ROI separately. The first assessed whether

each ROI distinguished between visual perspectives, regardless of visuotactile stimulation (see Figure 5A). The second tested for regions that distinguished between sync and async visuotactile stimulation, collapsed across visual perspective (see Figure 5B). To investigate the interaction between visual perspective and embodiment, a last target dissimilarity matrix assessed whether neural similarity in each ROI correlated with a linear relationship among conditions ranging from in-body sync to in-body async to out-of-body sync to out-of-body async (see Figure 5C). Thus, the linear contrast allowed me to test whether the selected ROIs were able to represent conditions on a continuum ranging from fully in-body (i.e. in-body sync) to fully out-of-body (i.e., out-of-body async).

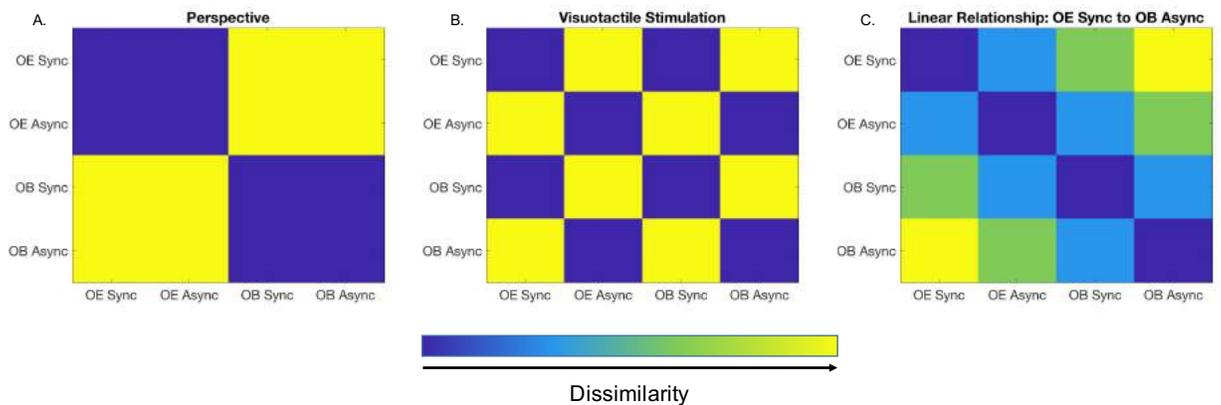


Figure 5. Target dissimilarity matrices used for each RSA. Dissimilarities between conditions were computed according to visual perspective (A), visuotactile stimulation (B), and a linear relationship ranging from OE sync to OE async to OB sync to OB async.

For the RSA, beta estimates from each functional run were averaged together for each condition, resulting in four beta estimates per condition. Next, neural dissimilarity within each ROI was estimated and compared to the three target dissimilarity matrices separately for each participant. These subject-level

correlations from each ROI were then Fisher-transformed to more closely approximate a normal distribution for statistical analysis. Multiple comparisons correction was implemented through threshold-free cluster enhancement, whereby an combined value for each voxel is calculated after a raw statistical map has been thresholded over an extensive set of values (Smith & Nichols, 2009). This approach capitalizes on the heightened sensitivity of cluster-based thresholding methods, without the limitation of defining an initial fixed cluster threshold a-priori (Oosterhoff, Connolly, & Haxby, 2016; Smith & Nichols, 2009), and is less affected by non-stationarity within data (Salimi-Khorshidi, Smith & Nichols, 2011). 10,000 Monte Carlo simulations were estimated to identify ROIs with correlations significantly greater than 0 (Oosterhoff, Connolly, & Haxby, 2016), resulting in one z-score per ROI corrected for multiple comparisons.

3.3.5.1 Target dissimilarity matrix model comparison. To determine which target dissimilarity matrix with significant correlations best fit the observed data, regression lines describing correlations between each significant target dissimilarity matrix and neural dissimilarity were calculated. *R*-squared values associated with each model were extracted and compared.

3.3.5.2 Whole-brain searchlight analysis. I conducted a wholebrain searchlight analysis to determine whether any additional areas outside of the specified ROIs contributed to the representation of visual perspective and/or level of embodiment using Normalized beta estimates from each functional run were averaged together for each condition, resulting in four beta estimates per condition. Next, a sphere comprised of 100 voxels was fitted around each voxel in the

acquired volumes to create searchlight maps for each participant. Neural activity was compared to each of the three target dissimilarity matrices differentiating conditions according to visual perspective, embodiment, or the linear relationship among conditions ranging from in-body sync to out-of-body async. Grand mean centring was implemented to remove main effects present across the data. Resulting correlation values were Fisher transformed to approximate a normal distribution. In order to investigate group-level effects, I conducted voxel-wise t-tests to identify correlations significantly greater than zero. A statistical threshold of $p < .005$ was implemented using family-wise error correction.

3.4 Results

3.4.1 Behavioral Results

The following behavioral analyses included the 11 participants excluded from the neuroimaging analyses due to excessive movement during scanning. When these participants were removed from the analysis, the results exhibited the same trend for the cued recall accuracy and subjective ratings obtained immediately following encoding, during scanning, and post-scanning.

3.4.1.1 Event encoding: OBEQ. A 2 x 2 x 2 repeated measures ANOVA with question type (illusion, control), visual perspective (in-body, out-of-body), and visuotactile stimulation (synchronous, asynchronous) as factors revealed a main effect of question type, $F(1,27) = 73.185$, $p < .001$, $\eta_p^2 = .730$, and visuotactile stimulation, $F(1, 27) = 12.025$, $p = .002$, $\eta_p^2 = .308$. Main effects were qualified by a two-way interaction between question type and visuotactile stimulation, $F(1,27) = 24.819$, $p < .001$, $\eta_p^2 = .479$. Illusion statement scores were higher in synchronous

($M = .946$, $SD = 1.349$) compared to asynchronous conditions ($M = -.274$, $SD = 1.111$), $p < .001$, demonstrating that the embodiment illusion was successful for both in-body and out-of-body perspective conditions. A separate two-way interaction was found between question type and perspective, $F(1,27) = 24.830$, $p < .001$, $\eta_p^2 = .479$, indicating that control statement scores were significantly more negative in in-body ($M = -1.86$, $SD = .884$) compared to out-of-body perspectives ($M = -.91$, $SD = 1.169$), $p < .001$. Effects were further qualified by a three way interaction between question type, perspective and embodiment, $F(1,27) = 10.984$, $p = .003$, $\eta_p^2 = .289$ (see Table 1 for means and standard deviations). Illusion scores associated with synchronous visuotactile stimulation were more positive in in-body compared to out-of-body perspectives, $p = .002$, indicating the embodiment illusion was stronger in the in-body perspective conditions. Moreover, control statement scores were more negative in in-body compared to out-of-body perspective conditions following both synchronous and asynchronous visuotactile stimulation, p 's $< .001$. Further, illusion statement scores were higher in synchronous compared to asynchronous conditions for both in-body, $p < .001$, and out-of-body perspectives, $p = .029$. For in-body perspectives only, control statement scores were more negative following synchronous compared to asynchronous visuotactile stimulation, $p = .020$.

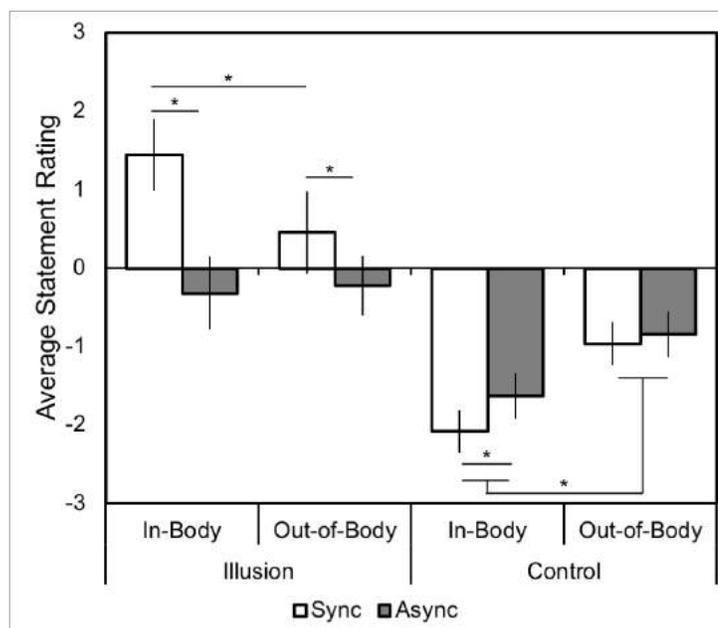


Figure 6. Results of the OBEQ. While illusion statement scores were higher for synchronous compared to asynchronous visuotactile stimulation for both perspectives, this effect was stronger for in-body perspectives. Control statement scores were more negative for in-body compared to out-of-body conditions, and for synchronous compared to asynchronous in-body conditions.

3.4.1.2 Immediate memory test. A 2 x 2 repeated measures ANOVA with visual perspective (in-body, out-of-body) and visuotactile stimulation (sync, async) conducted on average cued recall accuracy scores did not reveal any significant main effects or interactions. Thus, these findings suggest that there were no differences in immediate memory recall between conditions. To assess potential differences in perspective ratings between conditions, I conducted a 2 x 2 repeated measures MANOVA with visual perspective (in-body, out-of-body) and visuotactile stimulation (sync, async) as independent variables and in-body and out-of-body perspective ratings as dependent variables. As expected, there was a main effect of perspective, $p < .001$, Wilk's $\lambda = 26.509$, $\eta_p^2 = .495$, and visuotactile stimulation, $p = .043$, Wilk's $\lambda = 4.530$, $\eta_p^2 = .144$. Main effects were qualified by an interaction

between rating and perspective $p < .001$, Wilk's $\lambda = 67.595$, $\eta_p^2 = .715$. In-body ratings were higher for events encoded from an in-body perspective ($M = 5.897$, $SD = 1.185$) compared to an out-of-body perspective ($M = 3.795$, $SD = 1.412$) and out-of-body ratings were higher for events encoded from an out-of-body perspective ($M = 4.094$, $SD = 1.508$) compared to in-body perspective ($M = 1.759$, $SD = 1.418$), p 's $< .001$ (see Figure 7). I conducted an additional 2 x 2 repeated measures MANOVA with visual perspective (in-body, out-of-body) and visuotactile stimulation as independent variables and subjective ratings of vividness, emotional intensity, and perceived memory accuracy as dependent variables to assess potential phenomenological differences between conditions. No other significant main effects or interactions were observed.

Together, results indicate the visual perspective manipulation was successful in that participants could recall whether events were encoded from an in-body or out-of-body perspective immediately following memory encoding. Importantly, this did not lead to other changes in memory phenomenology, as vividness, emotional intensity, and perceived memory accuracy were equal across conditions.

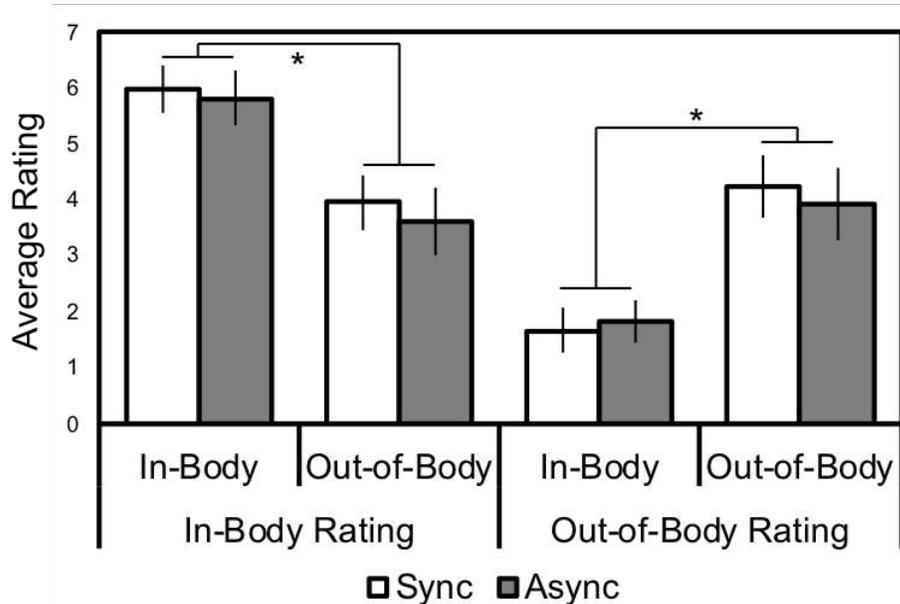


Figure 7. Session one visual perspective ratings. OE ratings were higher for events encoded from an OE perspective, while OB ratings were higher for events encoded from an OB perspective.

3.4.1.3 In-scanner subjective ratings. Perspective ratings were converted from a four-point scale used in-scanner to a seven-point scale to allow comparison with the perspective ratings measured during the immediate memory test. Then, a 2 x 2 repeated measures MANOVA with visual perspective (in-body, out-of-body) and visuotactile stimulation (synchronous, asynchronous) conducted on in-body and out-of-body perspective ratings identified a main effect of perspective rating, $p < .001$, Wilk's $\lambda = 22.779$, $\eta_p^2 = .458$, which was qualified by an interaction between perspective rating and perspective, $p < .001$, Wilk's $\lambda = 27.897$, $\eta_p^2 = .508$. As observed during the encoding session, in-body ratings were higher for events encoded from an in-body perspective ($M = 3.035$, $SD = .545$) compared to out-of-body perspective ($M = 2.522$, $SD = .661$), $p < .001$, and out-of-body ratings were higher for events encoded from an out-of-body perspective ($M = 2.258$, $SD = .635$)

compared to in-body perspective ($M = 1.760$, $SD = .503$; see Figure 8). A 2 x 2 repeated measures ANOVA with visual perspective (in-body, out-of-body) and visuotactile stimulation (synchronous, asynchronous) on vividness ratings did not reveal any significant main effects or interactions. Thus, these findings show that participants were able to recall the visual perspective events were encoded from during retrieval, while vividness remained equal across conditions.

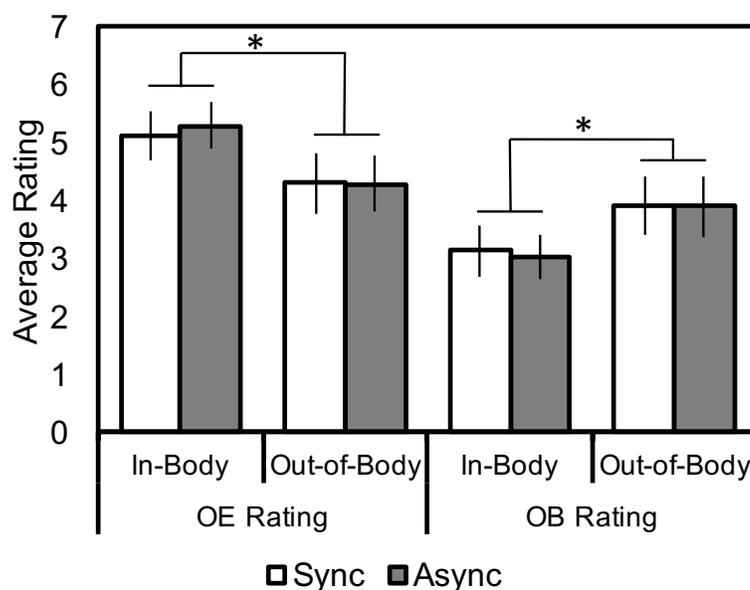


Figure 8. In-scanner visual perspective ratings. OE ratings were higher for events encoded from an OE perspective, while OB ratings were higher for events encoded

3.4.1.4 Post-scanning cued recall and subjective ratings. A 2 x 2 repeated measures MANOVA with visual perspective (in-body, out-of-body) and visuotactile stimulation (sync, async) conducted on average cued recall accuracy identified a significant interaction, $F(1,27) = 4.720$, $p = .039$, $\eta_p^2 = .149$. Cued recall accuracy was higher for synchronous in-body perspectives ($M = .964$, $SD = .090$) compared to both asynchronous in-body perspectives ($M = .902$, $SD = .122$) and synchronous

out-of-body perspectives ($M = .875$, $SD = .175$), p 's $< .05$ (see Figure 9). A 2 x 2 repeated measures MANOVA with perspective (in-body, out-of-body) and visuotactile stimulation (synchronous, asynchronous) on subjective ratings of emotional intensity and perceived memory accuracy did not find any significant main effects or interactions.

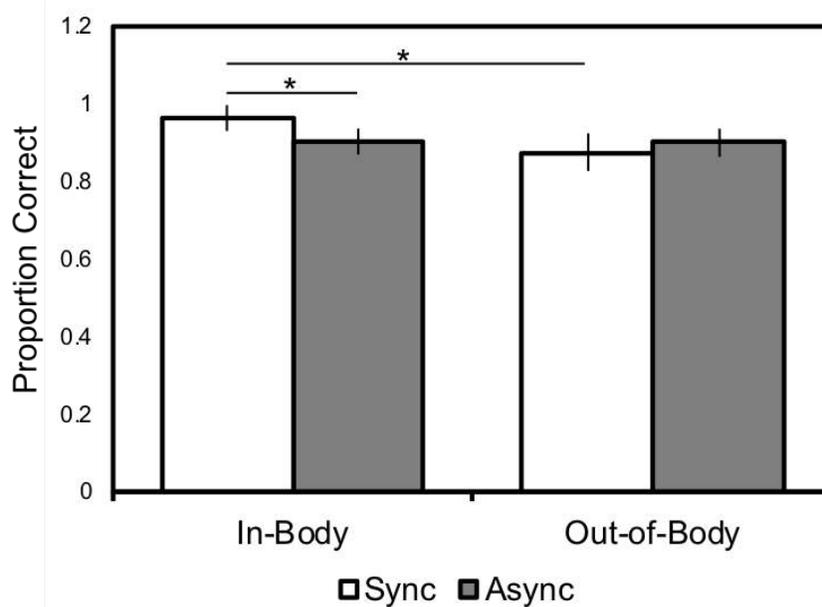


Figure 9. Post-scanning cued recall accuracy. Cued recall accuracy post-scanning was highest in the synchronous in-body condition compared to the asynchronous in-body and synchronous out-of-body conditions.

Thus, the embodiment illusion was successfully induced for both in-body and out-of-body perspectives, although the effect was stronger in the former. Moreover, while visual perspective was successfully recalled both immediately following memory encoding and during functional scanning, there were no differences in memory vividness, emotional intensity, or perceived memory accuracy in either testing session. Last, encoding events from a synchronous in-body perspectives led to increased cued recall accuracy post-scanning.

3.4.2 Representational Similarity Analyses Results

3.4.2.1 Visual perspective. To investigate whether visual perspective was represented in each of the ROIs, I compared neural dissimilarity in each ROI to a target dissimilarity matrix differentiating conditions according to visual perspective. Significant correlations were observed within posterior cingulate cortex, $z = 2.05$, $p = .02$, $\eta_p^2 = .23$, (see Figure 10A). Analyses conducted on the angular gyrus ($z = 1.02$, $p = .15$), hippocampus ($z = .00$, $p = .50$) and precuneus ($z = .0$, $p = .50$) were not significant.

3.4.2.2 Visuotactile stimulation. Neural dissimilarity within each ROI was compared to a target dissimilarity matrix differentiating conditions according to visuotactile stimulation to determine whether patterns of activity in the selected ROIs contained information related to sense of embodiment. I found a significant correlation in parahippocampal cortex ($z = -1.82$, $p = .03$, $\eta_p^2 = .18$). However, the negative z-score implies that the target dissimilarity matrix was consistently inaccurate at predicting neural dissimilarity. No additional correlations were significant (posterior cingulate cortex: $z = .00$, $p = .50$; angular gyrus: $z = .00$, $p = .50$; hippocampus: $z = .00$, $p = .50$; precuneus: $z = .00$, $p = .50$).

3.4.2.3 Linear relationship (In-body sync to out-of-body async). To test whether any of the ROIs represented interaction between visual perspective and embodiment, neural dissimilarity was compared to a target dissimilarity matrix defining a linear relationship between conditions ranging from a fully in-body (i.e., in-body sync) to fully out-of-body perspective (i.e., out-of-body async). This analysis revealed significant correlations in posterior cingulate cortex ($z = 2.88$, $p =$

.002, $\eta_p^2 = .46$) and the angular gyrus ($z = 1.88$, $p = .03$, $\eta_p^2 = .20$; see Figure 10B). Correlations obtained from the hippocampus ($z = .00$, $p = .50$, one-tailed) and precuneus ($z = .00$, $p = .50$) were not significant.

3.4.2.4 Whole-brain searchlight analyses. I did not find any clusters that survived multiple comparisons correction for the three whole-brain searchlight analyses comparing neural dissimilarity with each of the target dissimilarity matrices. Results indicate that no regions outside of the selected ROIs contained information representing visual perspective, embodiment, or the linear relationship among conditions ranging from fully in-body (in-body sync) to fully out-of-body (out-of-body async).

In sum, results of the representational similarity analyses indicate that both the angular gyrus and posterior cingulate cortex were able to represent conditions according to a linear relationship ranging from a fully in-body to a fully out-of-body perspective, while only posterior cingulate cortex was able to distinctly represent each visual perspective. Moreover, the visual perspective target dissimilarity matrix best accounted for the observed data.

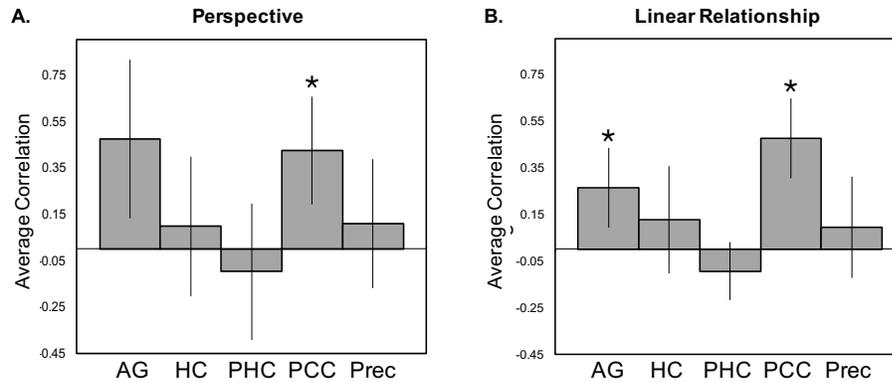


Figure 10. Average correlations between neural similarity and the target dissimilarity matrix differentiating conditions according to visual perspective (A). Average correlations between neural similarity and the target dissimilarity matrix specifying a linear relationship between conditions from a strong in-body to strong out-of-body perspective (B). AG = angular gyrus, HC = hippocampus, PHC = parahippocampal cortex, PCC = posterior cingulate cortex, Prec = precuneus. Error bars were calculated at the within-subjects level.

3.5 Discussion

The present study was conducted in order to understand how visual perspective and sense of embodiment are represented in a key set of regions underlying memory retrieval. Representational similarity analysis revealed that a model differentiating conditions according to visual perspective alone best explained the patterns of brain activity during memory retrieval. According to this model, posterior cingulate cortex was distinguished between in-body and out-of-body perspectives, although this pattern was also observed in the angular gyrus. Further, both posterior cingulate cortex and the angular gyrus were sensitive to the interaction between visual perspective and embodiment along a continuum from fully in-body (i.e., in-body sync) to fully out-of-body (i.e., out-of-body async). Importantly, the fMRI results were not influenced by initial differences between the

conditions in memory accuracy or phenomenological qualities of vividness, emotional intensity, and perceived memory accuracy, as these were equated during encoding. Together, the results help to elucidate how fundamental aspects of selfhood, namely the feeling of being located within and experiencing the world from the perspective of one's own body, are integrated within memory.

Visual perspective is a rare example of a purely self-specific process (Legrand & Ruby, 2009), and the feeling of having a body is a vital component of selfhood (Blanke, 2012). Thus, the finding that posterior cingulate cortex was able to distinctly represent in-body and out-of-body visual perspectives as well as the interaction between visual perspective and embodiment supports evidence that this region is distinctively involved in the processing of self-related information. For example, posterior cingulate cortex is active during successful memory retrieval (Addis, Wong, & Schacter, 2007; Fink et al., 1996; Rugg & Vilberg, 2013; Vann et al., 2009), and the incorporation of self-related stimuli within an autobiographical context (Northoff & Bermpohl, 2004). Moreover, posterior cingulate cortex is a core hub of the default mode network (Andrews-Hanna et al., 2010; Greicius, Supekar, Menon, & Dougherty., 2009; Margulies et al., 2009; Leech & Sharp, 2013; Leech, Kamourieh, Beckmann, & Sharp, 2011), whose activity reflects self-evaluative processing (Andrews-Hanna et al., 2010; D'Argembeau et al., 2008; D'Argembeau et al., 2005; Leech & Sharp, 2013). For example, Davey, Pujol, and Harrison (2016) identified ventral posterior cingulate cortex as the driver of activity within a 'core self' system, also including medial prefrontal cortex and intraparietal lobule. The authors asked participants to decide whether a specific trait applied to

themselves or not, and contrasted this against activity during rest. Ventral posterior cingulate cortex, medial prefrontal cortex, and the intraparietal lobule were recruited during both rest and self-referential judgments, but were also more active during the self-referential task. Dynamic causal modeling confirmed that activity within this 'core self' system was initiated predominately by activity of ventral posterior cingulate cortex. Posterior cingulate cortex has also been implicated in the retrieval of real and imagined autobiographical events, compared to retrieval of film and news clips unrelated to the self (Summerfield, Hassabis, & Maguire, 2008). Thus, previous research has linked activity in posterior cingulate cortex to evaluation of self-referential judgments and content. The results of the current study expand upon these findings by demonstrating that posterior cingulate cortex is also involved in the representation of self-specific information related to visual perspective.

Posterior cingulate cortex was also shown to represent visual perspective according to the level of embodiment, demonstrating for the first time that this region integrates two fundamental aspects of selfhood, namely the feeling of having a body and experiencing the world from a unique vantage point, within memories. Posterior cingulate cortex has previously been shown to combine bodily ownership with self-location to support unified feelings of bodily self-consciousness (Guterstam et al., 2015b). This study transferred participants' perceived self-location outside of their physical bodies to a mannequin during functional scanning using a similar illusion induction procedure as the present study. The authors found that the sense of self-location could be determined by multivariate patterns of

activity within posterior cingulate cortex. Additionally, successful decoding of self-location in the posterior cingulate cortex was linked to heightened effective connectivity with the intraparietal sulcus, hippocampus, and retrosplenial cortex associated with feelings of bodily ownership. These findings imply that posterior cingulate plays a crucial role in combining self-location with bodily ownership. This unified sense of bodily self-consciousness may help to represent the body's orientation within a larger spatial context, as lesions to posterior cingulate cortex result in heading disorientation, whereby individuals lose the ability to navigate based on relationships between their present location and landmarks (Aguirre & D'Esposito, 1999). Future research should directly test how feelings of bodily selfhood may contribute to navigation processes in order to better understand this relationship. Thus, while previous research has implicated posterior cingulate cortex in establishing bodily self-consciousness (Guterstam et al., 2015b), which may help to support navigation (Aguirre & D'Esposito, 1999), the present study is the first to show that bodily selfhood becomes integrated within a given visual perspective in this region to situate the self within memories.

In addition to posterior cingulate cortex, the angular gyrus was also found to represent visual perspective according to level of embodiment. The current results are consistent with a function of the angular gyrus that combines multisensory aspects of memories within a unified, egocentric (i.e., representing self-to-object relationships) scaffold, which enables subjective reliving during retrieval (Bonnici, Cheke, Green, Fitzgerald, & Simons, 2018; Bonnici, Richter, Yazar, & Simons, 2016; Ciaramelli et al., 2010; Yazar, Bergström, & Simons, 2017; Yazar,

Bergström, & Simons, 2014). The angular gyrus is a “convergence zone”, whereby multiple streams of information from different modalities are integrated (Damasio, 1989; Seghier, 2013; Shimamura, 2011). For example, Bonnici and colleagues (2016) recently demonstrated that the angular gyrus selectively represents multimodal, as opposed to unimodal, contents of episodic memories. In this study, participants were presented with either unimodal (i.e., either audio or visual) or multimodal (i.e., audio-visual) film clips that were later recalled during functional scanning. Angular gyrus activity was greater during retrieval of multimodal, as opposed to unimodal, memories. Additionally, multivariate analyses confirmed that individual multimodal memories could be decoded from patterns of activity in the angular gyrus, while information relating to distinct unimodal memories was absent. The results of the present study build on knowledge of the multisensory nature of the angular gyrus by showing that the type of multimodal information represented in this region extends beyond auditory and visual memory features reflecting external aspects of the environment during retrieval, to distinctly self-related aspects of memories, namely visual perspective and embodiment.

The current study also yields insights into the nature of egocentric representations stored in the angular gyrus. Previous research has argued that the angular gyrus is involved in establishing a first-person perspective in a mental scene through multisensory integration, which enables subjective remembering during retrieval (Bonnici et al., 2018; Bonnici et al., 2016; Ciaramelli et al., 2010; Yazar et al., 2017). Specifically, Bonnici and colleagues (2018) found that continuous theta burst stimulation applied to left angular gyrus reduces the

tendency to experience memories from an in-body perspective, demonstrating the causal role of this region in creating a unified first-person perspective during retrieval. This account is consistent with neuropsychological evidence demonstrating that disrupting angular gyrus activity through brain damage, (Ionta et al., 2011), seizures (Blanke et al., 2004), or transcranial magnetic stimulation (Blanke et al., 2002) is correlated with the occurrence of out-of-body experiences. Additionally, lesions in the angular gyrus are associated with reduced first-person-perspective imagery during navigation (Ciaramelli et al., 2010). Together, these studies suggest that the angular gyrus is necessary for establishing a cohesive in-body perspective from which to experience the world and re-experience memories. In contrast, the current findings demonstrate that angular gyrus represents both in-body and out-of-body perspectives according to the sense of embodiment, suggesting that this region is sensitive to differences between both types of visual perspectives and the bodily feelings that they elicit during retrieval. Representation of distinct visual perspectives linked to feelings of bodily selfhood within the angular gyrus can then be used to flexibly shift between visual perspectives, as has previously been reported (St. Jacques, Szupunar, & Schacter, 2017). Thus, the present study refines current conceptions of egocentric representations within the angular gyrus by demonstrating that this region is capable of representing information related to both in-body and out-of-body visual perspectives integrated with sense of bodily selfhood during memory retrieval.

Turning to the precuneus, I did not find evidence that this region represented visual perspective as initially predicted. This finding is consistent with

results on perspective shifting during memory retrieval (St. Jacques et al., 2018; St. Jacques et al., 2017), supporting the argument that this region is involved in manipulating mental images within an egocentric framework (Byrne, Becker, & Burgess, 2007). Such processes may be recruited more when people adopt an out-of-body perspective during retrieval of events encoded from an in-body perspective, which is more likely to require updating of internal representations of the world in order to retrieve memories from a novel self-location in space. In the present study, retrieving memories from an out-of-body perspective did not incur greater demands on mental transformation processes since events were encoded from an out-of-body perspective. Consequently, participants did not need to update their mental scene to fit a novel perspective. Thus, visual perspectives may not have been distinctly represented in the precuneus because this region is likely sensitive to demands placed on mental transformation of visual images, which have differed between visual perspectives in previous investigations (Grol et al., 2017; St. Jacques et al., 2018; St. Jacques et al., 2017). Future research that directly manipulates demands placed on mental transformation processes required to instantiate a novel in-body and out-of-body visual perspectives in a mental scene is an important next step in elucidating the role of the precuneus in memory retrieval.

The current study also did not find that the hippocampus was sensitive to information related to the visual perspective experienced during encoding. Previous research has found delayed activation of the hippocampus in response to retrieving memories for events encoded from an out-of-body compared to an in-

body perspective, which coincided with reductions in vividness and impaired memory for episodic details during retrieval (Bergouignan et al., 2014). Conflicting results may be due to methodological differences between studies. For example, whereas Bergouignan and colleagues (2014) introduced a two-week delay between memory encoding and retrieval, the present study investigated memory representations less than one-day old. The finding that neither visual perspective nor sense of embodiment associated with newly encoded events were represented in the hippocampus suggests that more time may be necessary to observe effects of these memory features within this region. Further, Bergouignan and colleagues (2014) found that reductions in vividness predicted delayed activation of the hippocampus. However, vividness was equal across conditions in the present investigation. Together, results from both studies suggest that memories encoded from an out-of-body perspective tend to lose their vividness over time, and that these differences in memory phenomenology are what contributed to delayed activation of the hippocampus reported by Bergouignan and colleagues (2014). A second methodological difference in my study that may explain why I did not find representation of visual perspective or embodiment in the hippocampus relates to the illusion induction procedure. Bergouignan and colleagues (2014) employed only synchronous visuotactile stimulation and compared average illusion statement ratings against average control statement ratings to assess the strength of the illusion induction. The authors concluded that the embodiment illusion was successful for both in-body and out-of-body perspectives since average illusion statement scores were higher than average control statement scores in both visual

perspectives. Here, I administered both synchronous and asynchronous visuotactile stimulation and compared average illusion statement score between the two types of visuotactile stimulation, as has frequently been reported by previous investigations on embodiment (e.g. Ehrsson, 2007; Guterstam et al., 2015a; Guterstam et al., 2015b; Petkova, Khoshnevis, & Ehrsson, 2011). Average illusion statement scores were higher following synchronous compared to asynchronous visuotactile stimulation for events encoded from an in-body perspective. However, in the current study there was no difference in illusion ratings for synchronous and asynchronous visuotactile stimulation for events encoded from an out-of-body perspective, indicating that feelings of bodily ownership, embodiment, and self-location were similar between visuotactile conditions. Thus, differences in activation of the hippocampus during memory retrieval in the study by Bergouignan and colleagues (2014) may have been due to methodological differences regarding the delay between memory encoding and retrieval, and induction of the embodiment illusion (i.e., only using synchronous visuotactile stimulation).

The current findings regarding cued recall accuracy are consistent with a small but growing body of literature that indicates memory accuracy is optimal when events are encoded from an embodied, first-person perspective. Here, I found that cued recall accuracy following repeated retrieval was higher for synchronous in-body perspectives, compared to asynchronous in-body perspectives and synchronous out-of-body perspectives. Similarly, Bergouignan and colleagues (2014) observed that encoding events from an in-body compared

to out-of-body perspective led to greater recall of episodic details. More recently, Bréchet and colleagues (2018) demonstrated that delayed recognition memory accuracy for immersive virtual scenes is enhanced when one's body is visible from a first-person perspective, compared to when it is invisible. Together, the results of these three separate studies strongly indicate that the body experienced from a first-person perspective plays an important role in enhancing objective memory accuracy performance.

The current findings add new insight regarding the importance of an in-body perspective in establishing sense of bodily selfhood, because I show for the first time that healthy individuals remain tethered to their physical bodies when viewed from a third-person perspective, despite conflicting multisensory information conveying an altered self-location. Here, I show that participants did not feel more embodied following synchronous compared to asynchronous visuotactile stimulation in the out-of-body perspective. Guterstam and colleagues (2015a) demonstrated the possibility of inducing ownership over an unseen, invisible body using a similar illusion induction procedure as employed by the present investigation. The important difference was that the participant's physical body was not visible in their field of view during the illusion induction. In my study, participants were able to see their bodies as if standing behind themselves, mimicking reports of clinical out-of-body experiences wherein a patient's real body is viewed from a third-person perspective (Blanke et al., 2004). My finding that feelings of bodily selfhood were similar following synchronous and asynchronous visuotactile stimulation for the out-of-body perspective is consistent with the finding

that experiencing an environment from an in-body perspective determines bodily ownership to a greater degree than visuotactile synchrony (Slater, Spanlang, Sanchez-Vives, & Blanke, 2010). The neural mechanisms that enable visual perspective to override bottom-up multisensory information in healthy individuals should be targeted by future research to inform understanding of out-of-body experiences in clinical disorders.

In sum, the present study combined the often separated fields of memory and embodiment to provide new insights into how an individual's unique perspective on the world and sense of bodily-self influence patterns of activity underlying retrieval. I found that posterior cingulate cortex was able to represent information relating to visual perspective and visual perspective according to level of embodiment, thereby demonstrating its role in the processing of self-related information. The angular gyrus was also found to represent visual perspective and embodiment along a continuum ranging from fully in-body to fully out-of-body, which refines current understanding of multisensory representations stored in this region that are unified into a consistent egocentric frame of reference during memory retrieval (Bonnici et al., 2018; Bonnici et al., 2016; Yazar et al., 2017). The lack of representation of visual perspective in precuneus informs current conceptions of this region's role in memory by highlighting a need to control for cognitive demands placed on mental transformation processes in neuroimaging studies of visual perspective. Finally, patterns of activity in the hippocampus were not found to reflect visual perspective or embodiment, emphasizing the importance of time and vividness in shaping memory representations during retrieval.

Ultimately, this line of research helps to elucidate how an elusive, multifaceted sense of self becomes incorporated within memories of the personal past.

**Chapter 4: Forming Memories for Events from Multiple Visual Perspectives in
a Virtual Environment**

4.1 Abstract

We typically experience the world from our own eyes (OE; i.e. first-person perspective), but can retrieve memories from an observer (i.e., OB; third-person perspective) viewpoint. Although we sometimes form observer memories, investigating these effects are hindered by our ability to manipulate perspective in realistic settings. Here, we developed an immersive virtual reality methodology to examine how perspective influences memory formation by projecting a virtual avatar into different virtual environments and changing the camera viewpoint fed to a head-mounted virtual reality display (i.e., Oculus Rift). Participants experienced virtual environments from OE and OB perspectives, and memory was tested immediately and following a one-week delay. OB perspectives were found to increase spatial memory accuracy immediately after encoding, due to a wider field of view afforded on a mental scene. I also found a bias in subjective ratings of perspective over time. Specifically, encoding events from an OB perspective increased self-reference and decreased mention of affective states in memory narratives over time. Moreover, OE perspective ratings increased between testing points, while OB perspective ratings decrease. These findings suggest that visual perspective at encoding is a key factor in determining objective and subjective memory qualities, which should be taken into account in future studies.

4.2 Introduction

Memories for events require adopting a particular visual perspective during both their formation and retrieval. This vantage point can either be from the perspective of one's own eyes (OE; i.e., first person perspective) or from an observer (OB) perspective in which one's physical body is visible from the outside (i.e., third person perspective; Nigro & Neisser, 1983). Visual perspective is a core aspect of memory that distinguishes remembering an event from having semantic knowledge of an event (Rubin & Umanath, 2015) and influences memory phenomenology (e.g. Bernstein & Rubin, 2006; D'Argembeau, Comblain & van der Linden, 2003; Mclaac & Eich, 2002; Sekiguchi & Nonaka, 2014; Sutin & Robins, 2010).

Previous research on visual perspective has typically assumed that memories in healthy individuals are strictly encoded from an OE perspective (e.g. Butler, Rice, Woolridge, & Rubin, 2016; De Brigard, 2014). In contrast, OB perspectives during encoding only tend to be associated with neurological damage (Blanke & Mohr, 2005) and dissociative disorders (i.e., schizophrenia, depression, anxiety; Blanke, Landis, Spinelli, & Seeck, 2004), which suggest an event was originally experienced from an out-of-body vantage point). However, Nigro & Neisser's (1983) seminal paper on visual perspective clearly states that while memories are typically formed from an own eyes perspective, "it is also possible to have observer experiences ... [whereby] we are conscious of how the entire scene would appear (or does appear in fact) to an onlooker who sees us as well as our surroundings" (p. 468). These OB perspective experiences in turn create OB

memories (i.e. memories for events encoded from an observer perspective). More recently, McCarroll (2016) has emphasized the strong likelihood of encoding events from an OB perspective, especially when the event contains high levels of self-conscious emotion or is traumatic. Further, OB perspective experiences are described as “normal, though unusual event(s)” (p. 163, Amorim, 2003), prevalent in 15% of the general population (Blackmore, 2017).

Little is known of how visual perspective during encoding influences memory processes, largely due to the fact that manipulating perspective at encoding has not been possible until recently. However, novel developments in virtual reality technology now allow researchers to easily manipulate visual perspective in realistic environments, offering a high level of ecological validity and experimental control. So far, virtual reality research has shown that own eyes perspectives are typically associated with higher sense of presence within virtual environments (Denisova & Cairns, 2015; Kallinen et al., 2007; Lim & Reeves, 2009;; though see Gorisse, Christmann, Amato, and Richir, 2017). Presence refers to the feeling of being “there” within a virtual environment, whereby one thinks, feels, and acts as though it were reality (Sanchez-Vives & Slater, 2005). Differences in presence according to perspective may influence how memories are formed within virtual environments. For example, higher presence in virtual environments viewed from an OE compared to observer perspective may influence subsequent memory phenomenology, which is known to influence the accuracy of retrieval (Marcotti & St. Jacques, 2017).

Apart from presence, visual perspective also influences spatial awareness (Gorisse et al., 2017) and navigation (Brunyé, Gardony, Mahony, & Taylor, 2012; Gorisse et al., 2017) in virtual environments. For example, Gorisse and colleagues (2017) first fitted participants with a virtual head mounted display (HMD) unit and a motion capture suit, then immersed them in virtual environments from either an OE or OB perspective. Participants were required to deflect a series of projectiles and jump between platforms to activate terminals without falling. The majority of participants subjectively preferred observer perspectives during the deflection task, consistent with previous research demonstrating that OB perspectives in virtual environments are perceived as more pleasant (Kallinnen et al., 2007). Moreover, perception of incoming projectiles was faster during immersion from an observer perspective, attributed to the wider field of view (FOV) compared to that afforded by the own eyes perspective. Thus, OB perspectives are associated with increased spatial awareness contingent on a wide FOV (Gorisse et al., 2017), which may influence objective spatial memory accuracy in the present investigation. However, OE perspectives facilitated spatial navigation (i.e., less time taken to reach target terminal), relative to OB perspectives. The advantage of OE perspectives on spatial navigation is corroborated by a separate study that asked participants to navigate between virtual landmarks from either an egocentric route perspective (i.e., own eyes perspective) or an allocentric survey perspective (i.e., bird's eye perspective, looking down on a virtual map; Brunyé and colleagues, 2012). Navigation between landmarks located close together was more efficient (i.e., closer to the optimal path between targets) when a route perspective was adopted,

supporting findings from Gorisse and colleagues (2017). Together, results from virtual reality research suggest that the visual perspective experienced as an event is unfolding may impact memory for the spatial layout of a scene.

Only one study to date has investigated the influence of visual perspective at encoding on memory. Bergouignan, Nyberg, and Ehrsson (2014) manipulated visual perspective at encoding by connecting a virtual reality HMD unit to a camera positioned either at the participant's physical location (i.e. OE perspective), directly behind and above the participant, or at a 30-degree angle to the participant's body (i.e. OB perspectives). The authors found that events encoded from an OB perspective were associated with impairments in retrieving spatial and temporal episodic memory details and reduced vividness during retrieval, correlated with delayed activation of the left posterior hippocampus. While this research offers a preliminary understanding of how visual perspective during encoding influences memory processing, it also leaves key questions unanswered. For example, Bergouignan, Nyberg, & Ehrsson (2014) tested recall of memory details with a semi-structured interview involving remember/know judgements, which subjectively assessed whether a given memory detail is recollected or familiar, but not the objective accuracy of the detail (Tulving, 1985). For instance, one may have a strong feeling of recollection associated with a particular memory, but incorrectly recall the specific episodic details of the event. Thus, how visual perspective at encoding influences objective memory accuracy has yet to be determined.

While research into the effect of visual perspective on memory encoding is limited, the literature focused on memory retrieval has shown robust effects of

visual perspective on phenomenology of recall (for review see Rice, 2010). For example, adopting an OE perspective during retrieval of complex lab-based events tends to direct attention inwards to experiential aspects of a memory, namely emotions, bodily sensations, psychological states, and associated ideas during memory retrieval (Bagri & Jones, 2009; McIsaac & Eich, 2002). Moreover, OE perspectives tend to be naturally adopted following instructions to focus on the feelings that arise during memory retrieval, as opposed to concrete contextual details (D'Argembeau, Comblain, & Van der Line, 2003; Nigro & Neisser, 1983), and when emotional compared to neutral memories are retrieved (D'Argembeau, Comblain, & Van Der Line, 2003). Moreover, Sutin and Robins (2010) observed that memories retrieved from an OE perspective are linked to increased vividness, coherence, and sensory detail. In contrast, OB perspectives in memory tend to focus on the retrieval of contextual information (Libby & Eibach, 2011), such as physical appearance of individuals, temporal order of events, and spatial locations of objects (McIsaac & Eich, 2002), at the expense of reduced sensory detail and emotion (Berntsen & Rubin, 2006). Thus, visual perspective biases access to different types of information (i.e. experiential vs. contextual) during retrieval, which impacts how a memory is relived.

Differences in phenomenology according to visual perspective have recently been found to further impact retrieval by influencing objective memory accuracy. Marcotti & St. Jacques (2018) had participants encode a series of lab-based events experienced from an OE perspective, which were later retrieved from either an OE or shifted OB perspective and assessed for memory accuracy through the

use of cued recall questions. Results across two experiments revealed that switching from an OE to an OB perspective led to reductions in vividness during subsequent retrieval, which in turn predicted reductions in memory accuracy. This study is the first to empirically demonstrate how visual perspective is capable of altering the objective precision of long-term memories. However, it is unclear whether these findings which relate to purposefully shifting visual perspective during retrieval will translate to the context of visual perspective at encoding.

The main aim of the present research was to investigate how visual perspective during memory encoding affects subsequent spatial and visual memory accuracy using a novel VR design across two studies. In Study One, participants were either assigned a virtual avatar or allowed to choose their own. Avatar selection was manipulated in light of previous research demonstrating that choice fosters a greater sense of self-identification with virtual avatars by boosting physiological responding (i.e. heart rate) to virtual events, especially for OB perspectives (Lim & Reeves, 2009). The more an individual self-identifies with their avatar, the more the individual should feel that the avatar was a proxy for themselves within the virtual environment, which should in turn strengthen effects of visual perspective at encoding on memory accuracy. Next, we projected participants into emotionally neutral, everyday virtual environments (i.e., café, house) experienced from an OE or OB perspective. Sense of presence was measured alongside spatial and visual memory accuracy immediately following memory encoding. Study Two was conducted in order to increase the level of immersion within virtual environments and level of self-identification between the

participant and their avatar, increasing the ecological validity of the present research. Further, a delayed testing session conducted one week after memory formation was included to investigate the influence of visual perspective at encoding over time.

For Study One, I predicted that spatial memory accuracy would be higher for events encoded from an OB perspective, as this perspective has been shown to facilitate recall of the spatial location of objects in memories (Mclsaac & Eich, 2002). In contrast, I predicted visual memory accuracy to be higher for OE perspectives based on previous findings of reduced accuracy of memories retrieved from an observer perspective (Marcotti & St. Jacques, 2018). Lastly, effects of visual perspective at encoding on memory accuracy are expected to be stronger when participants have a choice over their avatar selection, especially when their avatar is viewed from an observer perspective, given previous research showing that choice leads to higher levels of self-identification with the avatars viewed from a third-person vantage point (Lim & Reeves, 2009).

4.3 Methods: Study One

4.3.1 Participants

Participants included 50 healthy young adults (33 women, mean age in years = 21.80, SD = 2.59) with no prior history of neurological or psychiatric impairment. Participants were also not taking medications that affect mood or cognitive functioning. Each provided written consent in a manner approved by the School of Psychology at the University of Sussex. One participant was excluded due to virtual reality sickness.

4.3.2 Materials

Virtual environments, including a café and house, were downloaded from the Unity Asset Store. Visual details were then added and modified in terms of size and colour using Unity Engine 5.1.3 (Figure 1). For the café, I added cakes in the display case, travel mugs on the counter, a clock on the wall behind the counter, a garbage can by the bathrooms, as well as a tea set, teddy bear, handbag, newspaper, and present dispersed on various tables throughout the scene. On the street outside the café, I included a statue of a horse visible from the right café windows and adjusted the sky to resemble a sunset/sunrise. For the house environment, I created a birthday party scene by adding a large table in the living room that included a cake, plates, champagne, flutes, and party horns. The living room was further furnished with a wooden chair, desk with party hats, television and couch. Balloons of two different shapes and colours floating against the living room ceiling were also visible in the scene. I created a bedroom to the house which included a bed with a floral duvet, a bureau with flowers on top of it, and a chair. There was a library next to the library, where a chess board and a flower stand were inserted. Outside the house, I created a forest with a large, grassy hill in the distance. Lastly, the sky was changed to a starry night sky. Stimuli were viewed through an Oculus Rift DK2 HMD. This HMD has a resolution of 960 x 1080 per eye displayed at 75 Hz with 100° field of view. A package of four virtual avatars (i.e., two male, two female) were downloaded from the Unity Asset Store, which could be modified by the experimenter for skin tone and hair colour to match participants' physical appearance.



Figure 1. Screenshots from the virtual house (A) and café (B).

4.3.3. Procedure

Before testing, participants were asked to wear a plain white t-shirt and blue jeans to the laboratory to match the outfit of the virtual avatars, in order to strengthen self-identification between the participants and their avatars. A t-shirt was provided for participants that did not have one. There were two groups; one group was assigned an avatar to use throughout the experiment based on participants' gender ($N = 24$) while the other group chose among a selection of four avatars (two males, two females) that could be modified to match a participant's skin tone and hair colour ($N = 25$; Figure 2A). Avatar choice was manipulated in light of previous research demonstrating that it increases physiological responses within virtual environments (Lim & Reeves, 2009), which may influence memory phenomenology and accuracy in the present study.

During the study phase, participants were then seated in front of a desktop computer and fitted with the HMD to view the immersive VR environment. Visual perspective was manipulated using a within-subjects design by changing the camera location in the VR environment. Participants viewed the environments either from 1) an OE perspective, from the viewpoint of the avatar's eyes, or 2) an

OB perspective, located five metres behind the avatar (see Figure 2B). We used an incidental memory encoding procedure. Participants were asked to search for a red key in the virtual environment and were guided by the experimenter to explore and move around the environment (e.g., enter the café, stop just inside the door and look around; for full script see Appendix C). Participants used keyboard presses to move the avatar's body while the head tracking sensors in the HMD mapped head movements in real time. There was no red key in either environment.

Immediately after exploring each virtual environment, participants answered questions related to the degree of presence they felt within the virtual environment on seven-point Likert scales ranging from strongly disagree to strongly agree (see Appendix C; Usoh, Catena, Arman, & Slater, 2000). These questions were designed to target the three core components of presence, namely the participants subjective sense of “being there” inside the virtual scene, that the virtual scene was perceived as reality in contrast to the real world, and the sense that the virtual scene was a location visited as opposed to images on a screen (Sanchez-Vives & Slater, 2000). After answering the questions about presence, participants were given a two-minute break before entering the next test environment. The order of test environments and the perspective they were viewed from was counterbalanced across participants.



Figure 2. Participants were either assigned on of the two avatars on the right based on gender or selected an avatar among the four alternatives (A). FOV in OE (B) and OB conditions (C).

Following the study phase of both virtual environments, memory for each virtual experience was tested using a series of tests. First, narrative recall was assessed by asking participants to write a detailed description of their memory for each virtual environment. They were given up to five minutes to write the narrative for each environment. Second, spatial memory accuracy was assessed by asking participants to draw the spatial layout of each environment from a survey (i.e. bird's eye) perspective, as if they were looking down on the environment from above. Third, visual memory accuracy was assessed using cued-recall questions that pertained to either central or peripheral details of the virtual environment, presented in random order. Central details were defined as those aspects of the environment that directly related to the search task (i.e. questions about identity, number, and colour of objects placed where a key was likely to be hidden). Peripheral details referred to aspects of the virtual environment that did not related to the search task, such as the weather, time of day on the clocks, and colour of the walls.

4.3.4 Data Analysis

Spatial maps drawn by participants were coded based on a master spatial map that included the correct label and position of the test environments' features (i.e. furniture, doors, walls). One point was awarded for each correctly labelled feature in the correct position. Interrater reliability was assessed by calculating an intraclass correlation coefficient based on spatial memory accuracy scores obtained by myself and an independent rater on a randomly selected half of the

data. Cued recall questions were awarded one point per correct answer. To be coded as correct, answers were required to exactly match the detail addressed by the cued recall question (e.g., *What beverage was being served?* Correct Answer: *Champagne*, Incorrect Answer: *Wine*). Percentage of correct responses for central and peripheral details for both perspectives was calculated for each participant. Narrative accounts were analysed using Linguistic Inquiry and Word Count (LIWC; Pennebaker, Booth, Boyd & Francis, 2015), a text-analysis tool that assesses the frequency with which various categories of words are used. Here, I analysed the number of words related to perceptual processes associated with feeling (e.g., feels, touch), affect (i.e., words relating to positive emotion and negative emotions of anxiety, anger, and sadness), and personal pronouns (i.e., I, we, you, she/he, they).

4.4 Results: Study One

4.4.1 Presence

A mixed ANOVA with avatar choice (i.e., no choice, choice) as a between-groups factor and visual perspective (i.e., OE, OB) as a within-subjects factor on average presence ratings revealed a marginal main effect of perspective, $F(1,43)=3.57$, $p = .07$, $\eta_p^2 = .08$, suggesting higher presence for events encoded from an OE ($M = 4.07$, $SD = 1.16$) compared to OB perspective ($M = 3.60$, $S.D = 1.28$).

4.4.2 Memory Accuracy

The intraclass correlation conducted on spatial memory accuracy scores between raters was .95, indicating a high degree of interrater reliability. To examine the influence of visual perspective on spatial memory, we conducted a 2

(Visual Perspective: OE, OB) x 2 (Avatar Choice: yes, no) mixed ANOVA with avatar choice as a between-subjects factor and visual perspective as a within-subjects factor. There was a significant main effect of perspective, $F(1,47) = 6.17$, $p = .02$, $\eta_p^2 = .12$, indicating higher spatial memory accuracy in OB ($M = 51.26$, $SD = 17.44$) relative to OE ($M = 59.94$, $SD = 20.60$) conditions (see Figure 3).

Examples of the master spatial map for the house environment along with typical spatial maps drawn from each perspective can be found in Figure 4. The interaction between perspective and avatar choice was not significant (see Table 1 for means and SDs).

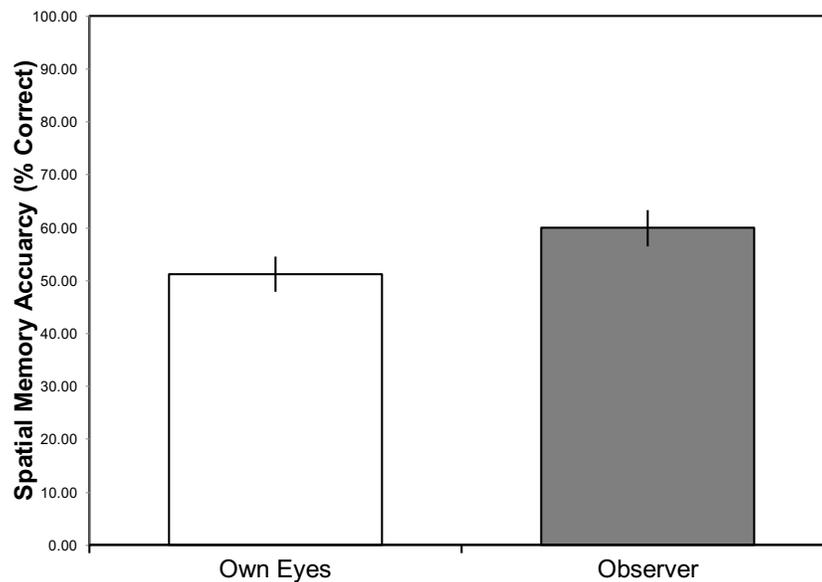


Figure 3. Spatial memory accuracy expressed as percent correct according to perspective. Error bars were calculated at the within-subjects level.

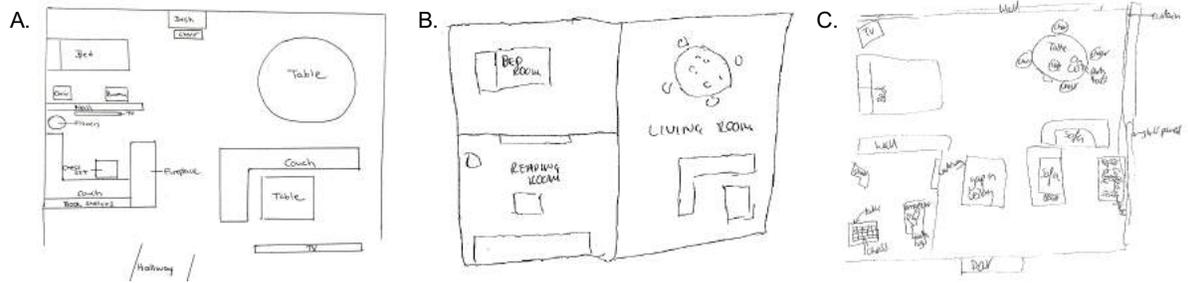


Figure 4. Master map of spatial layout of the the virtual house (A), compared against example maps drawn by participants from OE (B) and OB perspectives (B).

Table 1

Spatial Memory Accuracy (Percent Correct)

| | <u>Own Eyes</u> | <u>Observer</u> |
|---------------------------|-----------------|-----------------|
| No Choice | 52.86 (19.06) | 62.29 (17.30) |
| Choice | 49.71 (22.25) | 59.94 (17.44) |
| Mean (standard deviation) | | |

To examine how visual perspective influenced cued-recall accuracy, we conducted a 2 (Perspective: OE, OB) x 2 (Detail: central, peripheral) x 2 (Avatar Choice: yes, no) mixed ANOVA with avatar choice as a between-subjects factor and perspective and detail as within-subjects factors. We found a significant main effect of detail, $F(1, 47) = 9.65, p = .003, \eta_p^2 = .17$, indicating higher accuracy for central ($M = .45, SD = .14$) compared to peripheral ($M = .39, SD = .11$) details (See Figure 5). No other main effects or interactions were significant (see Table 2 for means and SDs).

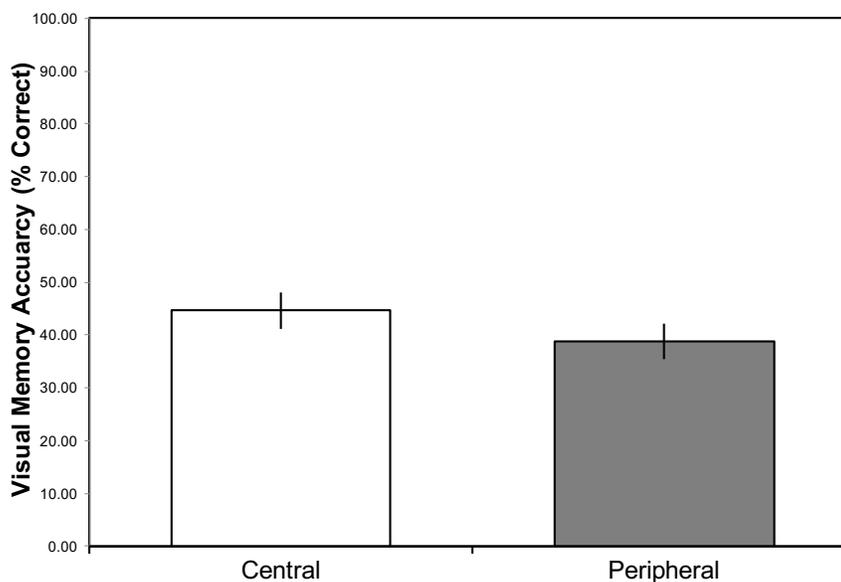


Figure 5. Visual memory accuracy expressed as percent correct according to detail level. Error bars were calculated at the within-subjects level.

Table 2

Visual Memory Accuracy (Percent Correct)

| | <u>Own Eyes</u> | <u>Observer</u> |
|---------------------------|------------------------|------------------------|
| Central Details | 45.00 (18.64) | 44.31 (16.56) |
| Peripheral Details | 41.50 (22.60) | 36.10 (25.31) |
| Mean (standard deviation) | | |

4.4.3 Narrative Recall

The output of the number of words related to perceptual processes associated with feeling in participants' memory narratives, affect, and pronouns extracted by the LIWC analysis were entered into separate mixed ANOVAs with perspective as a within-subjects factor and avatar choice as a between-subjects factor.

Turning to words related perceptual processes related to feeling, there was a significant main effect of perspective, $F(1,47) = 4.123$, $p = .048$, $\eta_p^2 = .081$, such that the OE perspective condition contained more words pertaining to feeling states ($M = 2.07$, $SD = 3.27$), compared to the OB perspective ($M = 1.10$, $SD = 1.79$). There was no interaction between perspective and avatar choice. Upon examining individual memory narratives, however, we noticed that several of the narratives included mentions of dizziness and/or nausea due to VR sickness ($N = 6$). Mentions of VR sickness were exclusively found in memory narratives of events encoded from an OE perspective. To control for this potential confound, we excluded instances related to VR sickness from the narratives and reran the LIWC analysis. The main effect of perspective on words related to perceptual processes associated with feeling did not remain after mentions of VR sickness. Neither of the analyses conducted on number of words relating to affect or personal pronouns found any significant main effects or interactions.

4.5 Discussion: Study One

The results of Study One indicate that presence was marginally higher for OE perspectives, suggesting that participants evaluated virtual environments experienced from this perspective as closer to reality relative to OB perspectives. Although visual memory accuracy was equivalent in both perspectives, spatial memory accuracy was higher for OB compared to own eyes perspectives. However, there was no effect of avatar choice. First, the finding of higher presence in virtual environments experienced from an OE perspective is consistent with previous research (Lim & Reeves, 2009; Denisova & Cairns, 2015). However,

results of the present study were only marginally significant, unlike the significant effects observed by previous investigations. This is likely due to the increased occurrence of VR sickness experienced by participants following immersion in virtual environments from an own eyes perspective, as evidenced by descriptions of nausea in memory narratives that were not present in narratives for events experienced from an observer perspective. VR sickness occurs when there is a mismatch between incoming visual information signalling movement in the virtual environment and internal signals indicating that the physical body is stationary (LaViola Jr, 2000). Increased incidence of VR sickness following immersion from an own eyes perspective may have inadvertently distracted participants from focusing on the main experimental task, thereby reducing the impact of perspective on presence. To eliminate the potential influence of VR sickness, Study Two employed real-time motion capture implemented with an Xbox Kinect camera that allowed participants to naturally move within the virtual environments, rather than navigate through keyboard presses. I predicted that OE perspectives would significantly increase sense of presence in virtual environments relative to OB perspectives, consistent with previous findings (Lim & Reeves, 2009; Denisova & Cairns, 2015).

Turning to the effect of visual perspective on memory, as predicted, spatial memory accuracy was higher for events encoded from an OB compared to an OE perspective. Previous research has demonstrated that OB perspectives during autobiographical memory retrieval lead to an increased focus on spatial aspects of a mental scene, such as the location of objects (McIsaac & Eich, 2002; Nigro &

Neisser, 1983). The present study extends upon previous findings by demonstrating that OB perspectives also lead to improved memory accuracy for the spatial layout of a scene. This effect is likely due to the wider FOV afforded by OB perspectives. Gorisse and colleagues (2017) found that engaging with a virtual environment from an OB perspective located above and behind a virtual avatar, as in the present study, led to improved spatial awareness due to a heightened ability to perceive objects in the periphery of the scene enabled by a larger FOV. Thus, the wider FOV for OB perspectives in the present study allowed participants to perceive more of the virtual scene, thereby improving retrieval of the spatial aspects of the virtual environment. To directly test whether this effect was dependent on the wider FOV in the OB perspective condition, FOV was held constant between visual perspectives in Study Two (see Figure 6). I predicted that spatial memory accuracy would no longer be higher following encoding from an OB compared to own eyes perspective, due to research demonstrating that increased spatial awareness associated with OB perspectives is contingent on a wider FOV (Gorisse et al., 2017).

Study Two



Figure 6. FOV was set such that the same amount of visual information was equal across visual perspectives.

Additionally, in Study Two I examined the influence of visual perspective on memory on both immediate and delayed retrieval tests. Changes in visual perspective during memory retrieval are linked to a loss of sensory information over time (e.g., Butler, Rice, Woolridge, & Rubin, 2016). Thus, effects of visual perspective on memory encoding may only emerge at a delay. Specifically, I predicted that visual memory accuracy would be higher for OE memories based on previous research showing that encoding events from an in-body perspective leads to enhanced recall of spatiotemporal and affective memory details (Bergouignan, Nyberg, & Ehrsson, 2014).

Finally, I also included subjective ratings of visual perspective, emotional intensity, vividness, and reliving in Study Two to understand how visual perspective at encoding influences memory phenomenology, as well as accuracy, and whether effects of visual perspective typically reported during memory retrieval are also found during encoding. Confirming Nigro & Neisser's (1983) concept of OB memories (i.e., the ability to form memories from an OB perspective), I expected that the visual perspective adopted during encoding would be the same as during

retrieval. I expected the effect of visual perspective at memory encoding on phenomenology to mirror previously established effects at retrieval, which reported increased emotional intensity, vividness, and reliving in own eyes compared to OB perspectives (Bernsten & Rubin, 2006; Mclsaac & Eich, 2002; Siedlecki, 2014; Sutin & Robins, 2010).

Avatar choice did not interact with visual perspective to influence memory accuracy in Study Two, possibly because participants did not identify with any of the four available options, thereby limiting self-identification with the selected avatar. To foster a stronger sense of self-identification between participants and their avatars, I created bespoke avatars to match each participant's appearance and administered a brief questionnaire on degree of avatar self-identification in Study Two. Before entering the main experimental virtual environment, participants were first immersed in a room containing a mirror directly ahead of the virtual avatar viewed from either an own eyes or observer perspective and asked to make a scripted series of movements. This allowed participants to see that their avatar's appearance resembled their own and that movement of the participant's body was mapped onto their avatar in real time. Motion capture also allowed participants to make natural movements within the virtual environments, increasing the ecological validity of the study.

In sum, several modifications to the study design were implemented in Study Two. First, FOV was held constant across perspectives so that each perspective had access to the same amount of visual information. Second, I included a delayed testing condition to investigate the influence of visual

perspective at encoding over time. Third, subjective ratings of perspective, emotional intensity, vividness, and reliving were included to assess potential differences in phenomenology according to perspective, which may have subsequent effects on memory accuracy. Lastly, customized avatars and motion capture were implemented to foster self-identification with the virtual avatars and increase the ecological validity of the study.

4.6 Methods: Study Two

4.6.1 Participants

Participants included 50 healthy young adults (32 women, mean age = 22.71, s.d. = 3.37) with no prior history of neurological or psychiatric impairment. Participants were not taking medications that affected mood or cognitive functioning. Each provided written consent in a manner approved by the School of Psychology at the University of Sussex.

4.6.2 Materials

Personalized avatars were built from recent photographs supplied by participants in advance of the experiment using Adobe Fuse CC (see Figure 7A), uploaded to Mixamo in the Adobe Creative Cloud, and imported into Unity Engine 5.2.2. During the testing session, each participant's movement was captured using Brekel Probody V1 linked to an Xbox Kinect camera positioned 1.2 metres in front of the participant (see Figure 7B). The location of the participant's joints was tracked in real time and projected onto the participant's avatar in the virtual environment. A training environment containing a virtual mirror was created so that participants could familiarize themselves with their avatar before entering the test

environments (see Figure 7C). Virtual test environments included the café and house from Study One, in addition to a classroom and an office downloaded from the Unity Asset Store. Modifications to the virtual classroom included adding a set of coloured pencils, a backpack, banana, textbooks, notebooks, paper, an eraser, backpack, and globe on top of various desks. Student desks behind the first row were deleted and replaced by a large table surrounded by chairs. An alphabet and periodic table poster were added to the walls. A swing set was placed in the courtyard outside the classroom visible from the windows and the sky was set to an overcast day. Modifications to the office included placing reading glasses, house plants, and water bottles on desks in the scene, a clock and world map on the walls, a laptop on a bench located near the window, a water cooler next to one end of the bench, and a large plant at the other end of the bench. Sky scrapers and a sunny sky with some white clouds were visible outside the window. Stimuli were viewed through an Oculus Rift DK2 HMD with the same settings as Study One.

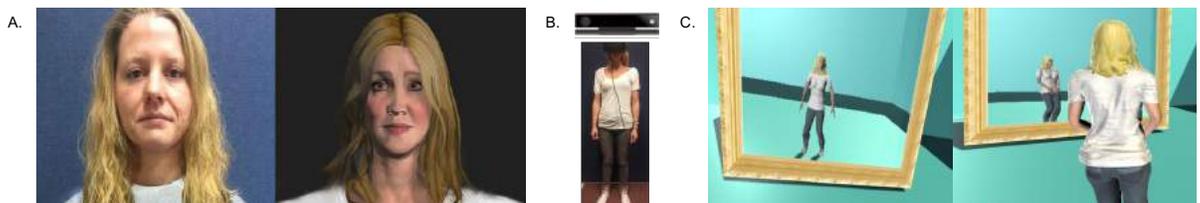


Figure 7. (A) Customized avatars were created to match the participant's appearance. (B) Motion capture was incorporated to increase the level of immersion with the virtual environments. (C) Participants familiarized themselves with their avatars by performing a series of scripted movements in front of a mirror before entering the test environment.

4.6.3 Procedure

The study involved two separate sessions spaced seven days apart. Before testing, participants were asked to wear a plain white t-shirt and blue jeans to the laboratory to match their avatars' outfits. A t-shirt was provided for participants that did not have one. During session one, participants wore the HMD and were initially placed on a marked position in the lab 1.2 metres in front of the Xbox Kinect motion capture sensor. Participants were then immersed inside a virtual training room whereby they could see the full body of their avatar from either an OE or OB perspective in a mirror. The OB perspective was positioned five metres behind the avatar at the same height as the own eyes perspective camera. FOV was held constant across both perspectives by moving the start position of the avatar in the OE perspective condition to the location of the camera in the OB perspective condition. Participants were then guided through a script specifying a series of movements (e.g. look down, pick up your right leg, take two steps towards the mirror, etc.) by the experimenter for 45 seconds (see Appendix C). Following this training phase participants were asked to close their eyes while the experimenter closed the training environment and opened the test environment, a period which lasted no longer than five seconds. The participant was then cued to open his/her eyes and visually search the virtual environment for a red key for a duration of two minutes. Participants were instructed to make head movements, but to remain on their mark (i.e. instructed not to walk) in order to control for the amount of movement between participants and minimize potential VR sickness. Participants were prompted to continue actively searching the virtual environment in the event

they were not making head movements. After the two minutes of visual search were complete, participants rated the degree of presence they experienced in the virtual environment using the same procedure as Study One. This process was repeated until the participant had experienced each of the four test environments. The order in which the test environments were presented and the perspective from which each was viewed was counterbalanced. Participants were given a two-minute break between test environments.

Participants were tested on two of the test environments (i.e. one encoded from an OE perspective, one encoded from an OB perspective) immediately following the encoding stage of the experiment. First, participants completed a narrative account of their memories for the specified virtual environment followed by spatial and visual memory accuracy tests in the same manner as Study One. Participants also completed subjective ratings of the degree to which an own eyes perspective was adopted during memory retrieval, the degree to which an OB perspective was adopted during memory retrieval, vividness, reliving, and emotional intensity on seven point Likert scales. Lastly, participants answered two questions related to how strongly they self-identified with their virtual avatar. These were “to what extent do you think your avatar actually resembles you?” and “to what extent did you identify with your avatar, as in you felt that you were the avatar in the virtual environment?”.

Seven days later, participants returned to the lab for session two where they completed the narrative accounts, tests of spatial and visual memory accuracy, and subjective ratings of perspective, vividness, reliving, and emotional intensity for

the virtual environments not tested during session one. Participants also filled out a series of questionnaires including the Perspective Taking / Spatial Orientation Test (Hegarty & Waller, 2004), the Paper Folding Test (Ekstrom, Dermen, & Harman, 1976), the Object-Spatial Imagery Questionnaire (Blajenkova, Kozhevnikov, & Motes, 2006), the Behavioural Identification Form (Vallacher & Wegner, 1989), Mark's Vividness of Mental Imagery Questionnaire (Marks, 1995), the Dissociative Experiences Scale (Bernstein & Putnam, 1986), and a questionnaire probing previous interaction with video games in terms of years of experience, hours of play per week, proportion of games spent playing from an own eyes perspective, and proportion of games spent playing from an observer perspective.

4.6.4 Data Analysis

Presence ratings, spatial maps, recall questions pertaining to visual memory accuracy, and memory narratives were assessed in the same manner as Study One. Interrater reliability of spatial memory accuracy was assessed by calculating intraclass correlations between scores recorded by myself and an independent rater on a randomly selected half of the participant sample.

4.7 Results: Study Two

4.7.1 Avatar Self-Identification Ratings

Participant responses from the two avatar identification questions were averaged together to obtain an overall avatar identification rating. The average avatar identification rating was 4.52 ($SD = 1.29$), indicating a moderately high level of self-identification with the virtual avatar.

4.7.2 Presence

A one-way repeated measure ANOVA on average presence ratings revealed a significant effect of perspective, $F(1,49) = 731.22$, $p < .001$, $\eta_p^2 = .94$, whereby sense of presence was higher when virtual environments were experienced from OE ($M = 4.42$, $SD = 1.22$) compared to OB ($M = 4.17$, $SD = 1.17$) perspectives (see Figure 8).

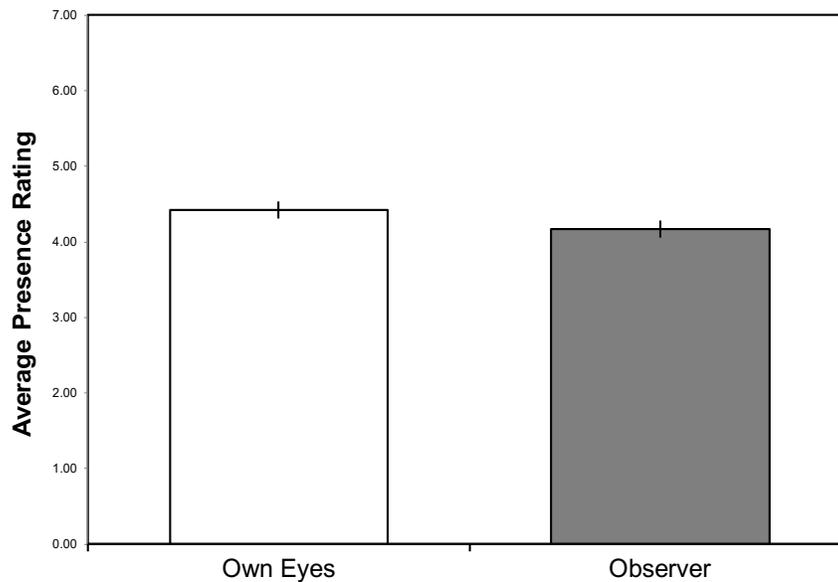


Figure 8. Average presence rating according to visual perspective. Error bars are calculated at the within-subjects level.

4.7.3 Memory Accuracy

The intraclass correlation coefficient between raters on spatial memory accuracy scores was .84, indicating high degree of interrater reliability. After controlling for FOV between perspectives, a two-way 2 (Perspective: own eyes, observer) x 2 (Testing Point: immediate, delayed) repeated measures ANOVA on

spatial memory accuracy scores did not reveal any significant main effects or interactions (see Table 3 for means).

Table 3

| <i>Spatial Memory Accuracy (Percent Correct)</i> | | |
|--|-----------------|-----------------|
| | Own Eyes | Observer |
| Immediate Testing | 39.60 (19.27) | 43.40 (19.02) |
| Delayed Testing | 39.20 (18.93) | 40.50 (16.23) |
| Mean (standard deviation) | | |

A three-way 2 (Perspective: OE, OB) x 2 (Testing Point: immediate, delayed) x 2 (Detail: central, peripheral) repeated measures ANOVA on visual memory accuracy revealed a significant main effect of detail, $F(1,49) = 37.67$, $p < .001$, $\eta_p^2 = .44$, indicative of higher accuracy for central ($M = 40.52$, $SD = 10.73$) compared to peripheral ($M = 29.25$, $SD = 12.07$) details (see Figure 9). A main effect of time was also observed, $F(1,49) = 11.52$, $p = .001$, $\eta_p^2 = .19$, revealing higher accuracy at immediate ($M = 38.46$, $SD = 11.54$) relative to delayed ($M = 31.31$, $SD = 12.42$) testing points (see Figure 10). The main effect of perspective was not significant, nor were any interactions between perspective, testing point, or detail.

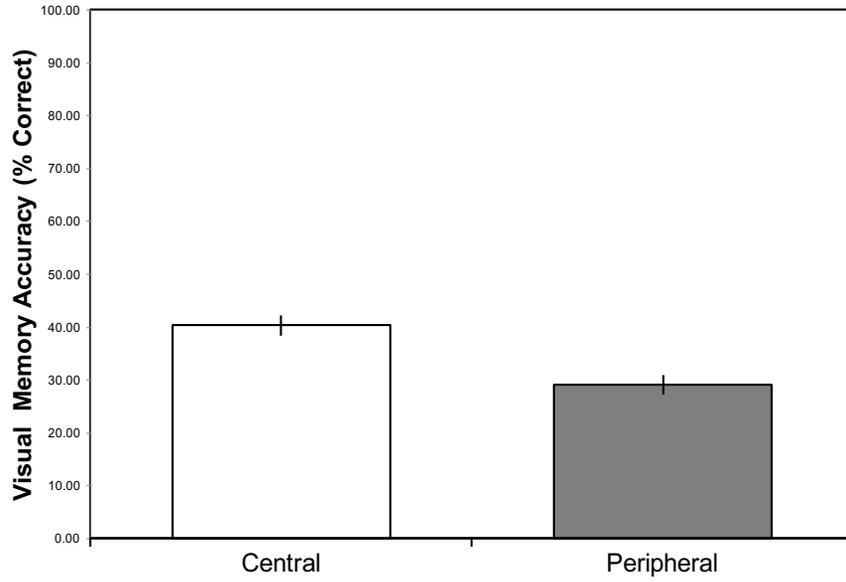


Figure 9. Visual memory accuracy, expressed as percent correct, according to testing point. Error bars are calculated at the within-subjects level.

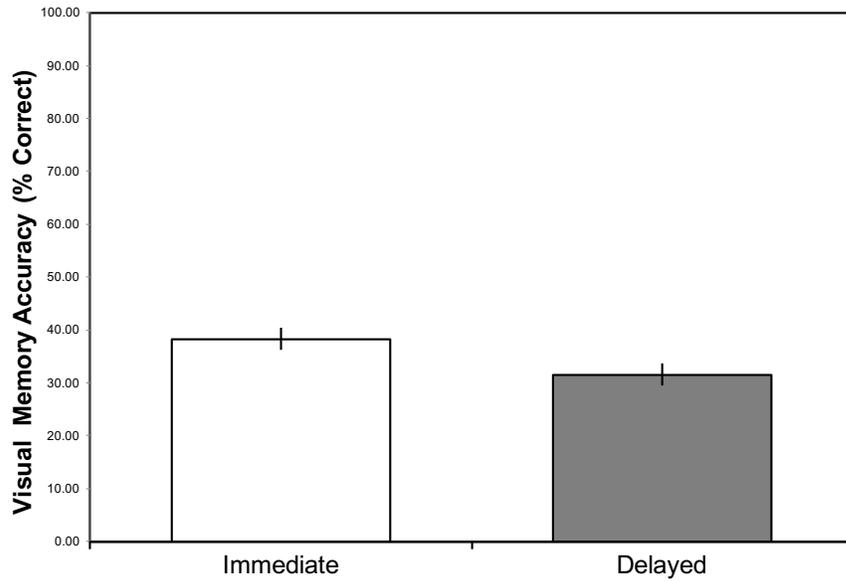


Figure 10. Visual memory accuracy, expressed as percent correct, according level of detail. Error bars are calculated at the within-subjects level.

4.7.4 Phenomenological Ratings

4.7.4.1 Perspective ratings. A three-way 2 (Perspective Rating: OE, OB) x 2 (Encoding Perspective: own eyes, observer) x 2 (Testing Point: immediate, delayed) repeated measures ANOVA revealed main effects of perspective rating, $F(1,49) = 41.49, p < .001, \eta_p^2 = .46$, and perspective, $F(1,49) = 4.12, p = .046, \eta_p^2 = .08$. Main effects were qualified by an interaction between perspective rating and perspective, $F(1,49) = 24.55, p < .001, \eta_p^2 = .33$, indicating participants had higher OE ratings for events encoded from an OE perspective, (OE: $M = 5.30, SD = 1.30$; OB: $M = 4.15, SD = 1.61, p < .001$) and higher OB ratings for events encoded from an OB perspective, (OE: $M = 2.29, SD = 1.33$; OB: $M = 3.77, SD = 1.58, p < .001$; see Figure 11). A subsequent interaction between perspective rating and time was also significant, $F(1,49) = 9.41, p = .004, \eta_p^2 = .16$. OE perspective ratings increased across testing points (Immediate: $M = 4.49, SD = 1.34$; Delayed: $M = 4.49, SD = 1.28, p = .03$), whereas OB ratings decreased across testing points (Immediate: $M = 3.40, SD = 1.47$; Delayed: $M = 2.66, SD = 1.22, p = .003$; see Figure 12).

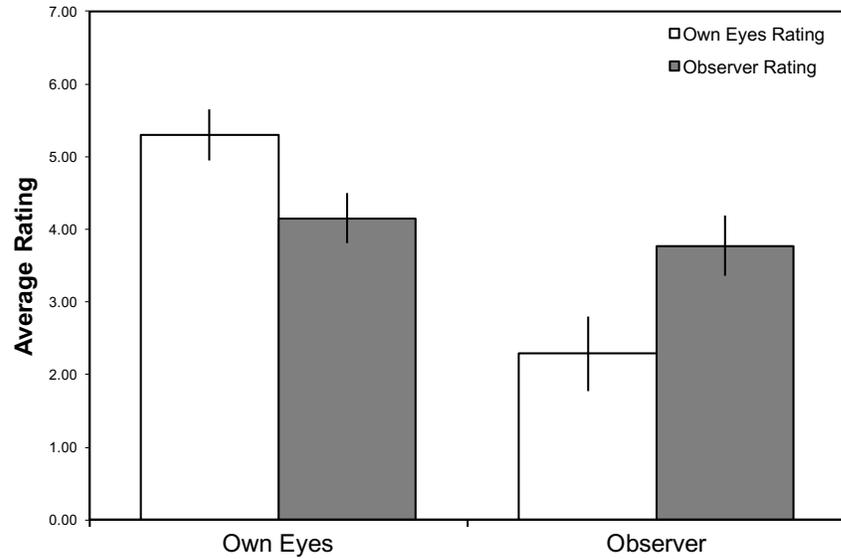


Figure 11. Average perspective rating according to encoding perspectives. Events encoded from an own eyes perspective received higher own eyes ratings, while events encoded from an observer perspective received higher observer ratings. Error bars are calculated at the within-subjects level.

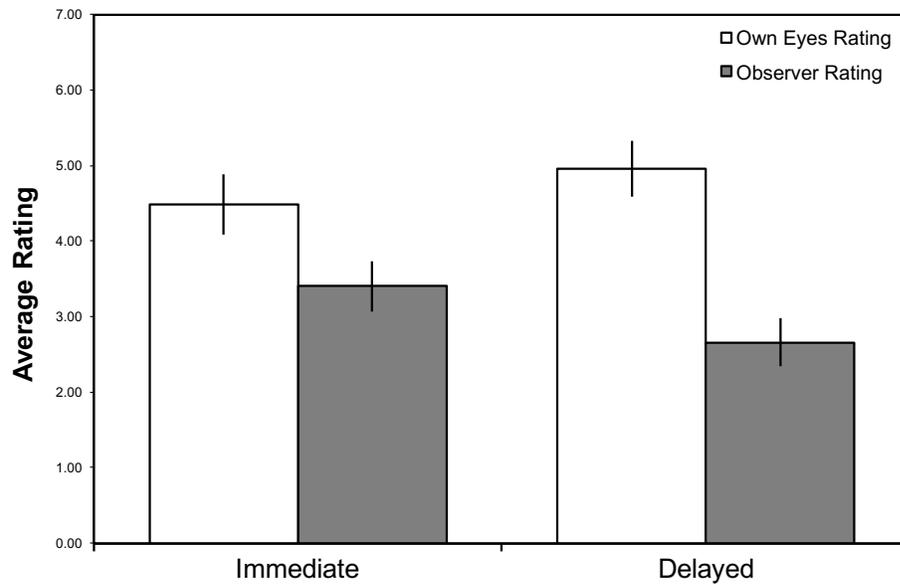


Figure 12. Average perspective rating according to testing point. While own eyes ratings increased over time, observer ratings decreased. Error bars are calculated at the within-subjects level.

4.7.4.2 Emotional Intensity, Reliving, and Vividness Ratings. A 3

(Rating: emotional intensity, reliving, vividness) x 2 (Perspective: OE, OB) x 2 (Testing Point: immediate, delayed) indicated a significant main effect of rating, $F(2,98) = 42.42, p < .001, \eta_p^2 = .46$, which was qualified by an interaction between rating and time, $F(2, 98), p = .008, \eta_p^2 = .10$. Follow up tests revealed a reduction in vividness over time (Immediate: $M = 4.12, SD = 1.15$; Delayed: $M = 3.48, SD = 1.10$). No other main effects or interactions were observed.

4.7.5 Narratives recall

The output of the number of words relating to perceptual processes associated with feeling, affect, and pronouns in participants' memory narratives extracted by the LIWC analysis were entered into separate two-way 2 (Perspective: OE, OB) x 2 (Testing Point: immediate, delayed). The analysis of words related to perceptual states related to feeling did not yield any significant main effects or interactions. However, the analysis conducted on words relating to affect found a marginally significant interaction between perspective and time, $F(1, 49) = 3.08, p = .09, \eta_p^2 = .06$ (see Figure 13). Post-hoc pairwise comparisons suggest that mention of affective states declined between immediate ($M = 1.32, SD = 2.04$) and delayed testing points ($M = 0.60, SD = .96$) for OB memory narratives.

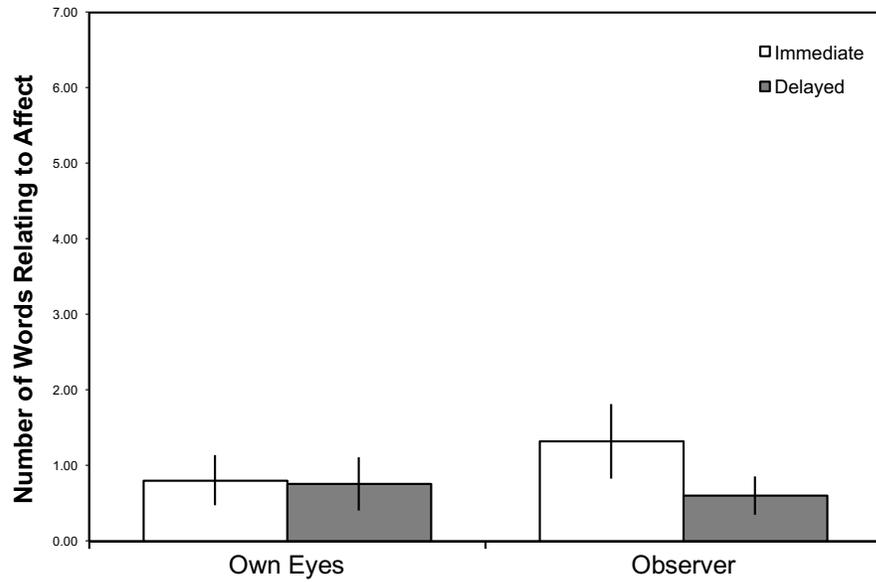


Figure 13. Number of words relating to affective states according to perspective and testing point. Number of words decreased across testing sessions for events encoded from an observer perspective. Error bars are calculated at the within-subjects level.

The analysis on number of personal pronouns found a significant main effects of perspective, $F(1,47) = 9.970$, $p = .003$, $\eta_p^2 = .175$, and time, $F(1,47) = 8.333$, $p = .006$, $\eta_p^2 = .151$, which were qualified by an interaction between perspective and testing point, $F(1,47) = 8.341$, $p = .006$, $\eta_p^2 = .151$. Mention of personal pronouns increased between immediate ($M = 4.90$, $SD = 3.63$) and delayed testing ($M = 7.81$, $SD = 5.88$) in memory narratives for events encoded from an OB perspective (see Figure 14).

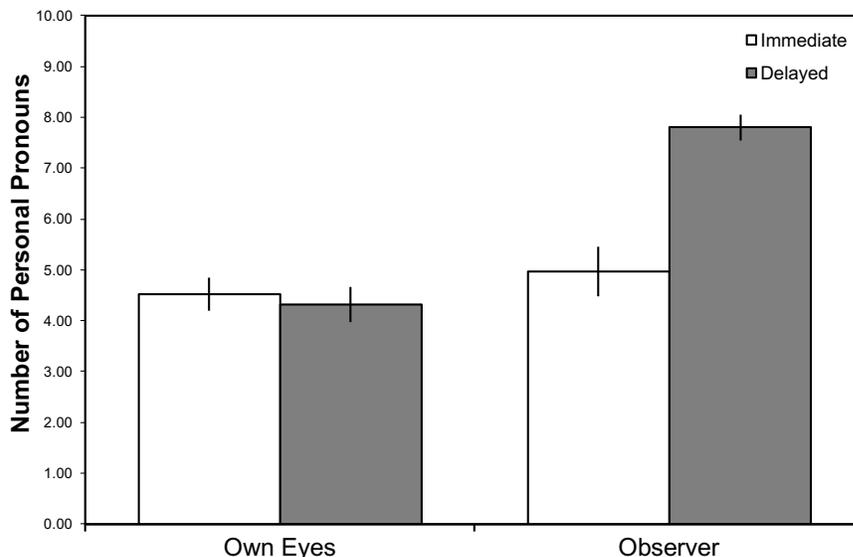


Figure 14. Number of words personal pronouns according to perspective and testing point. Personal pronoun use increased across testing points for observer perspectives. Error bars are calculated at the within-subjects level.

Altogether, the results of Study Two demonstrate that participants felt a moderate degree of self-identification with their avatar and experienced stronger presence within the virtual environments when immersed from an OE perspective. After controlling for FOV, spatial memory accuracy was similar across conditions. While visual memory accuracy was higher for central compared to peripheral details as well as immediate compared to delayed testing points, there was no effect of visual perspective. However, memory formation from an OB perspective decreased mention of affect alongside increased use of personal pronouns in memory narratives.

4.8 Discussion: Study Two

Study Two was conducted in order to investigate the effect of visual perspective at encoding on memory accuracy and phenomenology over time, while

increasing the level of immersion within virtual environments, strengthening participant's level of self-identification with their avatar, and controlling for FOV across visual perspectives. Results indicate visual perspective during encoding influences sense of presence in virtual environments, mention of words related to affect and personal pronouns in memory narratives over time, and visual perspective adopted during retrieval.

First, encoding of virtual environments from an OE perspective led to higher levels of reported presence. In contrast to the marginal effects observed in Study One, effects in Study Two are significant, likely due to the incorporation of motion capture software that allowed participants to move naturally within the virtual environments without being distracted by VR sickness. Naturalistic motion capture minimized the discrepancy between incoming visual information and internally derived kinaesthetic information. As a result, nausea related to VR sickness was greatly reduced in comparison to Study One and reported by only one participant. The results of the present study support previous research showing that the OE perspective leads to a stronger sense of presence within virtual environments, relative to OB perspectives (Lim & Reeves, 2009; Denisova & Cairns, 2015). Embodying a virtual avatar from an OE perspective allows one to "become" the avatar, whereas viewing it from an observer perspective as part of the virtual scene places focus on "controlling" it (Gard, 2000). Thus, virtual environments may feel more real when experienced from an OE perspective as it allows individuals to project their thoughts, behavior, and ownership onto their avatar (Denisova & Cairns, 2015).

While visual perspective influenced subjective measures of presence, it did not affect objective memory accuracy in Study Two. After controlling for FOV, spatial memory accuracy was no longer higher for events encoded from an OB perspective. Together, findings across studies suggest that OB perspectives enhance spatial memory accuracy by virtue of the wider FOV they afford. While previous research has found that OB perspectives engender higher spatial awareness in virtual environments linked to increased FOV relative to OE perspectives (Gorisse et al., 2017), the present study is the first to directly test and verify this association between visual perspective during memory formation and spatial memory accuracy. Regarding visual memory accuracy, neither study found an effect of visual perspective, demonstrating that visual perspective at encoding does not influence visual memory accuracy at retrieval. Rather, visual details central to the scavenger hunt task were recalled better than peripheral details, and there was a reduction in accuracy across delay intervals.

Visual perspective influenced the way that participants described their narratives. First, there was a decrease over time in the number of words related to affect in memories encoded from OB versus OE perspectives. This finding is similar to previous research linking observer perspectives in memory retrieval to a reduced focus on emotional states (Bagri & Jones, 2009; Bernstein & Rubin, 2006; Mclsaac & Eich, 2002; Nigro & Neisser, 1983). Here, the present study extends previous results by demonstrating that OB perspectives during memory encoding reduce the level of emotion with which memories are described at a delay. In contrast, mention of affective states remained stable across testing points for OE

perspectives, indicating a tendency for these memories to retain their emotional colouring. Second, OB perspectives led to an increase in the number of personal pronouns over time, indicating that adoption of this perspective during memory formation led participants to make reference to themselves and their avatars more frequently over time. Similarly, Sutin and Robins (2008) have highlighted the capacity for OB perspectives to increase visual attention to the self and heighten emotional intensity during autobiographical memory retrieval, relative to OE perspectives. Here, virtual events were emotionally neutral unlike autobiographical memories which tend to contain higher levels of affect, which potentially explains why emotional intensity was not affected by the visual perspective manipulation. Thus, present findings suggest that being able to see one's body from an observer perspective during memory formation can make the self especially salient during retrieval, leading to an increased use of personal pronouns in memory narratives.

As expected, visual perspective at encoding determined the perspective that people adopted during later retrieval. For both OE and OB perspectives, perspective at encoding matched perspective at retrieval. This finding validates the possibility of encoding event from OB perspectives, leading to the formation of OB memories (McCarroll, 2017; Nigro & Neisser, 1983). Although visual perspective was correctly recalled during retrieval, OE perspective ratings increased over time whereas OB perspective ratings decreased. Feeling self-located within a body provides an anchor for experience shown to establish a sense of bodily ownership (Petkova, Khoshnevis, & Ehrsson, 2011; Slater, Spanlang, Sanchez-Vives, & Blanke, 2010) and increase sense of presence (Lim & Reeves, 2009; Denisova &

Cairns, 2015). Reduction of OB ratings alongside increases in OE ratings over time in the present study further show that OE perspectives experienced from within an avatar's body also lead to resilient recall of encoding perspective, whereas loss of this bodily anchor during OB experiences results in less reliable recall of encoding perspective over time. An alternative explanation is that OE perspectives are more typical, and, thus, more robustly recalled with the passage of time. The OE perspective accounts for roughly two thirds of memories and is especially prominent in recent memories (Nigro & Neisser, 1983). The dominance of the OE perspective in everyday life may have led participants to make higher OE ratings during Session Two. At the same time, the unusual nature of an OB perspective during memory encoding could have reduced the degree to which the OB perspective was used when retrieving memories after a delay.

In sum, Study Two indicates that visual perspective at encoding influences the sense of presence within virtual environments, the way in which memories are described over time, and visual perspective adopted at retrieval.

4.9 General Discussion

The current study investigated the influence of visual perspective at encoding on sense of presence, memory accuracy and phenomenology. Across two studies, OE perspectives engendered a higher sense of presence in virtual environments, while OB perspectives were found to increase spatial memory accuracy by allowing access to more visual information in a scene. Further, OB perspectives affected how memories were described at a delay by decreasing words related to affect and increasing use of personal pronouns. Additionally, the

same visual perspective at encoding was adopted at retrieval, although the strength of perspective at retrieval increased for own eyes perspectives and decreased for observer perspectives over time.

First, sense of presence was higher following immersion in virtual environments from an OE perspective, compared to an OB perspective. OE perspectives lead to the feeling of “becoming” the virtual avatar, as opposed to “controlling” it when viewed from an OB perspective (Gard, 2000), which affects body ownership. For example, Petkova, Khoshnevis, & Ehrsson (2011) performed a body swap illusion where participants wore an HMD connected to a camera that provided either an OE or OB perspective on a mannequin’s body. The authors then stroked both the participant’s actual body and the mannequin’s body in corresponding locations either synchronously or asynchronously. Synchronous visuotactile stimulation typically elicits a sense of illusory ownership over the mannequin’s body, whereas asynchronous visuo-tactile stimulation does not, due to the multisensory nature of neural systems underlying bodily selfhood (e.g. Ehrsson, 2007; Lenggenhager, Tadi, Metzinger, & Blanke, 2007). Interestingly, transfer of bodily ownership, as measured by physiological reactions and questionnaire responses, was only possible when the mannequin was viewed from an OE perspective. Similarly, a separate study conducted by Slater, Spanlang, Sanchez-Vives, & Blanke (2010) found that an OE perspective was the strongest factor in establishing bodily ownership over a virtual avatar, compared to synchronous visuotactile stimulation and voluntary control over the avatar’s head movements. Collectively, this line of research on bodily ownership and avatar use

in virtual environments suggests that the OE perspective lead to a sense of bodily ownership, which allows one to project one's own experiences to a body that is not one's own, resulting in greater sense of presence within virtual environments.

Visual perspective also influenced memory accuracy in addition to sense of presence, such that the spatial layout of the virtual environment was more correctly retrieved when an observer perspective was adopted during memory formation. Only one other study has investigated the influence of visual perspective at encoding on memory, which focused on subjective characteristics of memories as opposed to objective memory accuracy (Bergouignan, Nyberg, & Ehrsson, 2014). Participants experienced a realistic social interaction while wearing a virtual reality headset live-linked to a camera positioned to create OE and OB perspectives, and sense of embodiment was created through a standard approach involving synchronous visuotactile feedback. The authors found that encoding memories from an OB perspective decreased the strength of recollection associated with temporal and spatial memory details and delayed recruitment of the posterior hippocampus, when compared to memories encoded from an OE perspective. Here, I adopted a more objective approach, assessing spatial memory accuracy by having participants draw spatial layouts of virtual environments and visual memory accuracy through cued recall questions. Together, results suggest that OB perspectives during encoding reduce the subjective sense of recollection associated with a memory (Bergouignan, Nyberg, & Ehrsson, 2014), while increasing spatial memory accuracy (present investigation).

Studies of visual perspective on objective memory accuracy have focused on effects at retrieval, rather than encoding. For instance, Bagri and Jones (2009) asked participants to read a series of passages detailing imaginary tasks and later write narratives while mentally reinstating the tasks from either an OE or OB perspective. The authors found that details concerning physical sensations, associated ideas, affective reactions, and psychological states were more accurately recalled when an own eyes perspective was adopted during retrieval of the imaginary events. However, they did not find an effect of visual perspective on spatial memory accuracy reported in the present investigation. Thus, the function of visual perspective may be different during encoding and retrieval stages of memory processing. The only other study to investigate the influence of visual perspective at retrieval on accuracy had participants encode a series of complex lab-based events from an OE perspective in an initial session, and subsequently retrieve memories for these events while either maintaining an OE perspective or switching to an OB perspective (Marcotti & St. Jacques, 2018). The effect of perspective shifting on memory accuracy was then assessed in a final session where participants answered cued recall questions related to details of the events. Shifted OB perspectives resulted in reduced memory accuracy as indexed by lower cued recall accuracy scores, relative to OE perspectives, linked to reductions in vividness. The lack of significant effect of perspective on memory accuracy in the present study combined with the results of Marcotti and St. Jacques' (2018) investigation again suggest that the function of visual perspective may vary according to encoding and retrieval phases of memory processing. Alternatively,

shifting away from the visual perspective adopted during memory encoding may instead be the cause of reduced memory accuracy observed by Marcotti and St. Jacques (2018), implying that OB perspectives are not inherently less accurate. However, this hypothesis has yet to be tested as no study to date has investigated the effects of shifting to an OE perspective during the retrieval of events encoded from an OB perspective on memory accuracy, and only two studies including the present investigation have manipulated visual perspective during encoding. Thus, future research should be undertaken to clarify the impact of visual perspective at encoding versus retrieval on memory accuracy to better understand how this core component of memories for events affects memory quality.

Turning to how visual perspective influenced memory phenomenology, the visual perspective adopted at encoding was the same at retrieval, which speaks to the possibility of encoding events from both OE and OB perspectives (McCarroll, 2017; Nigro & Neisser, 1983). While the vast majority of previous research on visual perspective has assumed that memories in healthy individuals are strictly encoded from an OE perspective (e.g., Butler, Rice, Woolrdige, & Rubin, 2016; De Brigard, 2014), there are certain situations that foster OB perspectives as an event is being experienced (McCarroll, 2017; Nigro & Neisser, 1983). For example, OB perspective experiences are commonly reported among patients with social phobia (Clark, 2001), especially in social contexts laden with anxiety (Wells & Papageorgiou, 1999). Moreover, Mclsaac and Eich (2004) found that nearly 40% of participants who had undergone traumatic incidents reported experiencing the event from an OB perspective as it was unfolding. A separate study by Cooper,

Yuille, & Kennedy (2002) investigated visual perspective at encoding by asking participants “Were there moments when you felt as though you were a spectator watching what was happening to you – for example, did you feel as if you were floating above the scene or observing as an outsider?” (p. 84) as they recalled memories for positive events, a sexual assault, and a non-sexual trauma. The authors found that participants endorsed a greater number of OB perspective experiences for the non-sexual traumatic events and concluded that it is possible for individuals to experience events from both OE and OB perspectives. Lastly, there are everyday situations in healthy individuals that lead to OB perspective experiences (McCarroll, 2017). Specifically, events involving strong levels of self-conscious emotion, such as when one is being observed or evaluated, promote detachment from the event as it is unfolding (McCarroll, 2017; Nigro & Neisser, 1983), further leading to OB perspective mental imagery during encoding (Rice, 2010). Hence, cases of social phobia, traumatic incidents, and everyday events incurring high levels of self-conscious emotion are capable of creating OB perspective experiences. The results of the present study demonstrate the viability of forming OB memories in healthy participants imply a strong need for future investigations to question the assumption that memories are always encoded from an OE perspective and further investigate the circumstances that lead to observer experiences during memory formation (e.g. presence of self-conscious emotions). Present findings also emphasize that healthy individuals are capable of having OB memories, indicating that these experiences are not necessarily of a clinical nature

(Cardena & Spiegel, 1993; Blanke, Landis, Spinelli, & Seeck, 2004; Blanke & Mohr, 2005).

Implications of my findings are limited by the extent to which participants treated their avatars as themselves within the virtual environments, which is necessary in order to extrapolate effects to the real world. Participants reported moderately high levels of self-identification with their virtual avatars in Study Two, indicating that they felt the avatar represented themselves reasonably well within the virtual environments. The development of novel techniques that project an image of a participant's actual body into a virtual environment rather than an avatar (e.g., Bréchet et al., 2018) stands to increase the ecological validity of virtual reality research moving forward. A second potential limitation is that I assumed OB perspectives inherently enable a wider FOV on a given scene when naturally adopted outside of the laboratory, which has yet to be empirically tested. Thus, future research should directly investigate FOV in memories from OE and OB perspectives to determine whether effects of visual perspective on spatial memory accuracy extend beyond virtual reality to the real world.

In sum, across two studies visual perspective during memory encoding was shown to influence sense of presence within virtual environments and spatial memory accuracy, contingent on FOV. Findings imply a need for future research to take into account the possibility of encoding events from an OB perspective and potential effects on objective and subjective memory characteristics.

Methodologically, the present studies demonstrate the power of virtual reality to examine research questions that were previously not amenable to investigation by

allowing the manipulation of visual perspective during memory formation. Further research directed at a deeper understanding of how visual perspective influences memory in virtual environments will lead to important insights not only relevant to the field of memory research, but also to VR developers who aim to better understand how their work impacts human experience and memory in a society where immersive technology is increasingly prominent.

Chapter 5 – General Discussion

The aim of this thesis was to shed new light on how visual perspective shapes the formation and retrieval of memories to advance understanding of how this core element of selfhood becomes integrated within memories for the personal past. Chapter One provided an overview of current conceptions of visual perspective in determining behavioral and neural correlates of memory formation and retrieval. In Chapter Two, I demonstrated the central role of visual perspective in guiding memory retrieval by showing how the adoption of different visual perspectives in autobiographical memories (AMs) influenced the timing, recruitment, and functional connectivity of underlying neural mechanisms. In Chapter Three, I investigated how encoding memories from in-body and out-of-body perspectives impacted neural representations of visual perspective and bodily selfhood during retrieval. Chapter Four expanded upon the role of visual perspective during encoding by showing how observer (OB) perspectives influence memory accuracy and the way past events are described over time. The ensuing discussion will show how the studies in this thesis yield novel insights into (1) theoretical models of perspective during memory encoding and retrieval, (2) the understanding of how visual perspective influences memory content, phenomenology, and accuracy, (3) neural mechanisms underlying memory retrieval from multiple visual perspectives, and (4) how bodily selfhood interacts with visual perspective to structure memories of past events.

5.1. Theoretical Accounts of Visual Perspective in AM

5.1.1. Memory Formation

Research on visual perspective in AM largely assumes that events are encoded from an own eyes (OE) perspective except in cases of brain damage (Blanke & Mohr, 2005) and clinical disorders (Blanke, Landis, Spinelli, & Seeck, 2004; Spiegel, Koopman, Cardeña & Classen, 1996), however, there is evidence to suggest that memories are formed from OB perspectives (McCarroll, 2018; 2017; Nigro & Neisser, 1983). During an OB perspective experience, one is able to see oneself in an environment as if from a point of view external to one's physical body as an event is unfolding. Chapters Three and Four capitalized on recent advances in virtual reality that enable manipulation of visual perspective during encoding to create OB perspective experiences in a laboratory setting. In these studies, participants either saw themselves (Chapter Three) or self-relevant avatars (Chapter Four) from OE and OB perspectives as they encoded realistic events. These experiments were designed to mimic "normal, though unusual" OB perspective experiences in real life (p. 163, Amorim, 2003), reported in 15% of the general population (Blackmore, 2017), and 25% of university students (Metzinger, 2005). Advances in virtual reality technology that allow for the manipulation of visual perspective and the encoding of realistic events in a highly controlled setting offers an exciting opportunity to study the phenomenon of OB perspective experiences, and the importance of occupying an embodied, OE perspective on the world to memory and selfhood.

I specifically investigated OB perspective experiences that involved a visual image of oneself in a scene from a location outside of the physical body. However, McCarroll (2018) raises the interesting conjecture that OB perspective experiences need not necessarily involve vision, opening up new lines of investigation for future research. Other modalities beyond the scope of vision contain information related to perspective (Wittgenstein, 1964/1975), which can be either internally or externally derived (McCarroll, 2018). For example, internal information related to kinaesthesia (i.e. awareness of bodily movement), proprioception (i.e., awareness of body position), and interoception (i.e., awareness of the body's internal state) can convey a specific perspective within a scene. External information relating to perspective can concern sensory information connected to olfaction, audition, and haptic processing, in addition to vision (McCarroll, 2018). These different types of information that convey perspective are accessible as an event is unfolding and can be used to construct "more benign" OB perspective experiences without the visual experience of seeing one's body as detached from one's visual perspective on a scene (p. 91, McCarroll, 2018). This idea aligns with the basic systems account of episodic memory that outlines how sensory, spatial, kinaesthetic, and affective information is dynamically integrated during retrieval (Rubin, 2006). McCarroll (2018) extends the implications of this model to memory encoding by claiming that the presence of multimodal streams of information during perception allow one to step outside of one's physical body, thereby creating OB perspective experiences. Chapter Three investigated one type of non-visual information related to perspective by investigating how feelings of embodiment that tie an individual to

a specific location in space during memory encoding affect neural mechanisms of retrieval, which will be addressed in section four of this discussion. However, further research into other types of multimodal information that convey a specific perspective on the world is required to understand how OB perspective experiences are constructed from information outside of the visual domain.

OB perspective experiences during memory encoding are theorized to lead to the adoption of OB perspectives during memory retrieval (Nigro & Neisser, 1983; Rice, 2010), yet empirical evidence of these observer memories is lacking as previous investigations have not been able to manipulate visual perspective during encoding until recently (Bergouignan, Nyberg, & Ehrsson, 2014; Bréchet et al., 2018). Chapters Two and Three address this gap in the literature by corroborating the concept of OB memories. Across these studies, I showed that events encoded from an OB perspective were recalled from the same perspective during retrieval both immediately following memory formation and after a week's delay. Thus, the viability of creating OB perspective experiences in the lab that are later retrieved from an OB perspective implies a need for research on visual perspective in memory to reconsider the assumption that memory formation in healthy individuals only occurs from an in-body, OE perspective (e.g. Butler, Rice, Woolridge, & Rubin, 2016; De Brigard, 2014), and directly investigate situational and individual factors that contribute to observer perspective experiences (McCarroll, 2018; 2017).

5.1.2 Memory Retrieval

Existing theoretical models of visual perspective have highlighted how OE and OB perspectives can be used to reflect distinct aspects of a past event, ultimately supporting a flexible, yet coherent, sense of self (Libby & Eibach, 2011; Sutin & Robins, 2008). While these models apply to visual mental imagery during memory retrieval and reconstructive processes linked to counterfactual and future episodic thinking, the present thesis underscores a need to broaden the scope of these models to consider visual perspective at encoding, as well as retrieval. In particular, Libby and Eibach (2011) construe OE and OB perspectives as separate representational tools used to frame a past event in complementary ways. They contend that OE perspectives focus an individual on tangible, sensory features of an event, which frames the self as an experiencing subject within a mental scene. In contrast, OB perspectives incorporate information not initially included in the original event to integrate it within a broader context, which frames the self as a conceptual object. Accordingly, the authors' model of visual perspective as a representational tool predicts that memory retrieval from an OE perspective will be accompanied by heightened sensory detail. This prediction is consistent with the finding of increased vividness in AMs retrieved from an OE perspective, compared to OB perspective (Chapter Two). However, behavioral results of Chapters Three and Four imply a need for theoretical models of visual perspective to consider the influence of encoding perspective on subsequent retrieval processes due to perspective. In these studies, visual perspective at encoding matched the perspective adopted at retrieval (i.e., events encoded from an OE perspective were

retrieved from an OE perspective; events encoded from an OB perspective were retrieved from an OB perspective). Thus, reported vividness should have been higher for memories retrieved from an OE visual perspective consistent with portraying the self as an experiencing subject as opposed to conceptual object, according to Libby and Eibach's (2011) model of visual perspective as a representational tool. However, there were no differences in reported vividness during retrieval of events encoded from OE and OB perspectives in these studies. Moreover, while Libby and Eibach (2011) predict that OE perspectives should be associated with a heightened focus on bodily reactions to events within a retrieved memory, I did not find differences between visual perspectives in terms of reported physical sensations in memory narratives, after controlling for mentions of virtual reality sickness in Chapter Four. The lack of differences in vividness and mention of bodily sensations within memory narratives according to visual perspective (Chapters Three and Four) suggest that visual perspective at encoding is an important factor in shaping retrieval of memories from a particular perspective.

Whereas memory retrieval from an OE perspective is thought to cast the self as an experiencing subject within an event, memory retrieval from an OB perspective frames the self as a conceptual object in the aim of facilitating a broader understanding of the event outside of bodily, affective, and psychological reactions (Libby & Eibach, 2011). Consistent with this idea, OB perspectives can heighten self-focused attention during retrieval, facilitating self-referential processing in memories (Sutin & Robins, 2008). Evidence from this thesis aligns with previous ideas linking OB perspectives to increased saliency of self. In

Chapter Two, I demonstrated that encoding events from an OB perspective led to an increased use of personal pronouns at delayed compared to immediate testing, while self-reference in memory narratives from OE perspectives did not change. This finding aligns with theories of visual perspective that link OB perspectives in memory retrieval to an increased awareness of the self as an object in a mental scene (Libby & Eibach, 2011; Sutin & Robins, 2008). Hence, my finding that viewing oneself from an OB perspective during memory formation can increase self-reference within memories over time extends Sutin and Robins (2008) model beyond memory retrieval to incorporate perspective at encoding.

In sum, this thesis informs theories on the role of visual perspective in memory formation by corroborating the existence of OB memories, and emphasizes that visual perspective at encoding must be taken into account when assessing the impact of visual perspective on retrieval. Together, the findings underscore the (re)constructive processes inherent to memory retrieval and formation, which ultimately contribute to a dynamic, yet enduring sense of self. Having discussed the theoretical implications of this thesis, I now develop these ideas further with a more in-depth consideration of how visual perspective influences memory phenomenology and quality.

5.2 Effects of Visual Perspective on AM Content, Phenomenology, and Accuracy

Research concerning the behavioral effects of visual perspective in memory have shown that visual perspective biases the type of information recalled during

retrieval, linking OE perspectives to bodily, affective, and psychological details, and OB perspectives to a focus on contextual memory features (e.g. Bagri & Jones, 2009; Bernstein & Rubin, 2006; D'Argembeau, Comblain, & Van der Line, 2003; Mclsaac & Eich, 2002; Nigro & Neisser, 1983). Consistent with this idea, vividness was higher for events retrieved from a typical OE perspective compared to typical OB perspective during AM retrieval (Chapter Two). Further, mention of affective states in memory narratives decreased between immediate and delayed testing points during retrieval of events encoded from an OB perspective, demonstrating the importance of time in determining the influence of visual perspective on memory phenomenology (Chapter Three). Together, these findings support arguments that OE perspectives tend to involve increased sensory and affective information during memory retrieval, relative to OB perspectives (e.g., Bagri & Jones, 2009; Bernstein & Rubin, 2006; Mclsaac & Eich, 2002). However, additional evidence from this thesis demonstrates that the relationship between OE perspectives and subjective feeling states in memories is not so clear cut. OB perspectives need not necessarily be "phenomenally dry" (i.e., lacking in affective and sensory memory features; p. 541, Fernández, 2014), indicating a need to rethink the role of visual perspective in determining the subjective experience of retrieval. Specifically, there were no differences in emotional intensity according to visual perspective during the retrieval of AMs (Chapter Two). Further, encoding memories from OE and OB perspectives resulted in equivalent levels of vividness and emotional intensity (Chapters Three and Four), and mention of physical sensations in memory narratives (Chapter Four) during retrieval. Thus,

experiencing events from either an OE or OB perspective supports the formation of events with sensory and affective information, and subsequent retrieval of rich phenomenology detail from both visual perspectives (McCarroll, 2018; McCarroll & Sutton, 2017). Consistent with this idea, OB perspectives adopted during retrieval are capable of heightening the emotional intensity of an event during memory retrieval if a past self is congruent with the present self (Sutin & Robins, 2008). For example, if a person believes themselves to be a poor public speaker, then retrieving a memory of a public presentation from an OB perspective will heighten self-focused attention, and consequently, increase feelings of anxiety associated with the memory (Sutin & Robins, 2008). In Chapter Two, I controlled for potential differences in emotional intensity associated with familiar places, which may have influenced the level of emotion in memories associated with these locations, and the events in Chapters Three and Four were emotionally neutral. Therefore, effects reported in this thesis could change for more emotional events.

Findings of this thesis yield insight into the influence of visual perspective on objective memory accuracy, in addition to content and phenomenology. Recently, Marcotti and St. Jacques (2018) found that shifting to an OB perspective during the retrieval of complex lab-based events led to reduced accuracy in retrieving sensory, visual, and spatial memory features, predicted by decreases in vividness. However, I found that visual perspective did not affect the accuracy with which visual or episodic details were recalled (Chapters Three and Four), but rather boosted spatial memory accuracy, contingent on a wider field view afforded upon a mental scene (Chapter Four). These findings show that OB perspectives do not

necessarily impair retrieval of visual details and can even enhance the retrieval of spatial aspects of a memory. The key difference between the studies in this thesis and the investigation conducted by Marcotti and St. Jacques (2018) concerns how events were encoded. Whereas participants in Chapters Three and Four encoded events from OE and OB perspectives and later retrieved memories for these events from the same perspective, Marcotti and St. Jacques (2018) asked participants to shift to an OB perspective during the retrieval of events originally encoded from an OE perspective. This important methodological difference provides a potential explanation for the discrepant findings between studies by suggesting that the effect of visual perspective on objective and subjective memory qualities may vary between encoding and retrieval. Alternatively, shifting away from the visual perspective adopted during memory encoding, rather than shifting to a particular OE or OB perspective, may instead be the cause of reduced memory accuracy observed by Marcotti and St. Jacques (2018). However, no study has yet tested the effects of shifting to an OE perspective during the retrieval of events originally encoded from an OB perspective.

Only two previous studies have manipulated visual perspective during memory encoding (Bergouignan, Nyberg, & Ehrsson, 2014; Bréchet et al., 2018). Bergouignan and colleagues (2014) found that retrieval of events encoded from an OB perspective is associated with impoverished recall of spatiotemporal and affective memory details (Bergouignan, Nyberg, & Ehrsson, 2014). However, Bergouignan and colleagues (2014) did not measure the visual perspective adopted during memory retrieval, which precludes determination of whether visual

perspective at encoding or shifts in visual perspective during retrieval affected recollection of episodic details. Similarly, Bréchet et al., (2018) found that experiencing an environment from an OE perspective that includes a view of one's body leads to improved recognition memory accuracy for elements within the scene, relative to occupying a disembodied perspective where one's body is not visible. However, in contrast with Chapter Four of the thesis, Bréchet and colleagues (2018) did not also include an OB perspective condition where the participant's body was visible from this perspective. Thus, it is unclear whether viewing one's body within a scene from an OE perspective specifically, or viewing one's body regardless of visual perspective, influences recognition memory.

In sum, this thesis advances our understanding of the effect of OB perspectives on subjective and objective aspects of memory formation. I have shown that OB perspectives are not necessarily associated with reductions in sensory and affective components (Chapters 2-4), as is commonly reported (e.g., Bagri & Jones, 2009; Bernstein & Rubin, 2006; D'Argembeau, Comblain, & Van der Linden, 2003; Mclsaac & Eich, 2002; Nigro & Neisser, 1983) and are likely due to changes in memories over time that were originally encoded from an OE perspective. Further, the adoption of OB perspectives during memory retrieval does not necessarily impair memory objective memory accuracy (Chapters Three and Four), as has previously been reported (Bergouignan et al., 2014; Marcotti & St. Jacques, 2018). In fact, OB perspectives have the capacity to improve retrieval of spatial memory features, by affording a wider field of view on a mental scene compared to OE perspectives (Chapter Four). Next, I turn to a consideration of

how this thesis has generated new insight into how visual perspective influences neural mechanisms of memory retrieval.

5.3 Neural Correlates of Visual Perspective in AM Retrieval

A main aim of this thesis was to advance understanding of the neural mechanisms that support visual perspective during AM retrieval. My findings shed light on the role played by medial temporal lobe (MTL) and posterior parietal regions in supporting visual perspective in memory. First, I found that typical OE perspectives were associated with greater functional connectivity between the hippocampus and an extended MTL network implicated in the visualization of mental scenes (Andrews-Hanna et al., 2010; Benoit & Schacter, 2015; Kahn, Andrews-Hanna, Vincent, Snyder, & Buckner, 2008; Madore, Szupunar, Addis & Schacter, 2016; St. Jacques et al., 2011), relative to both typical and atypical OB perspectives (Chapter Two). These findings are consistent with previous reports of greater integration in the MTL network among individuals who spontaneously recalled AMs from predominately OE perspectives (St. Jacques, Kragel, & Rubin, 2013). Together with the finding that OE perspectives involved increased activation of a core AM retrieval network including the hippocampus during late stages of retrieval, my results suggest that OE perspectives are better able to tap into key networks underlying AM retrieval during memory elaboration (Chapter Two). In contrast, adopting OB perspectives during AM retrieval placed greater demands on spatial transformation processes required to adapt the layout of the mental scene to accommodate the novel perspective, as indexed by early functional connectivity

between the hippocampus and posterior medial network associated with the construction of mental scenes (Ranganath & Ritchey, 2012), during memory retrieval and imagination (Robin, 2018). Results of Chapter Two demonstrate that visual perspective guides functional connectivity of the hippocampus during AM retrieval, emphasizing spatial transformation processes required to instantiate OB perspectives during construction and the greater capacity of OE perspectives to access declarative memory processes during elaboration.

In Chapter Three, I did not find that the hippocampus was involved in representing visual perspective during retrieval of events encoded from different visual perspectives. This result contrasts against previous reports that encoding memories from an OB perspective leads to repetition enhancement effects across repeated memory trials in the left posterior hippocampus (Bergouignan et al., 2014). One reason may be due to changes in memories encoded from OE and OB perspectives that emerge over time. Whereas Bergouignan and colleagues (2014) studied memories that were two weeks old, the memories in my study were retrieved on the same day as encoding, implying that more time may be necessary in order for the effects of visual perspective to manifest in the hippocampus, related to changes in memory phenomenology. Supporting this idea, Bergouignan and colleagues (2014) found a reduction in vividness ratings during retrieval after a delay. Additionally, I also found that subjective aspects of memories encoded from different visual perspectives changed over brief periods of time, as retrieval of events encoded from an OB perspective reduced the tendency to retrieve events from an OB perspective and increased self-reference within memory narratives one

week after encoding (Chapter Four). Thus, increasing the delay between encoding and retrieval may lead to changes in memory phenomenology, such as the reduced vividness during retrieval of events encoded from an OB perspective reported by Bergouignan and colleagues (2014), which could then influence recruitment of the hippocampus during retrieval. Thus, findings within this thesis demonstrate that visual perspective influences how and when the hippocampus communicates with key memory retrieval networks (Chapter Two), which is likely dependent on changes in memory phenomenology that occur over time (Chapter Three).

Turning to posterior parietal regions, my results suggest that there are three key regions involved in supporting visual perspective. First, the precuneus during AM retrieval is linked to the manipulation of mental images from both types of visual perspectives, dependent on demands placed on spatial transformation processes required to adapt the spatial layout of a mental scene to match a given perspective. For example, I found that adopting atypical OB perspectives during AM retrieval was related to increased functional connectivity between the hippocampus and precuneus during early stages of retrieval when spatiotemporal contextual details are combined in order to construct a coherent mental scene (Chapter Two). This finding aligns with theories suggesting that egocentric frameworks generated during long term memory retrieval within the precuneus can be manipulated and updated when people imagine the movements they make within a remembered scene, based on allocentric (i.e., object to object) representations stored in MTL regions such as the hippocampus (Byrne, Becker, &

Burgess, 2007). Such processes may be recruited more when individuals adopt an OB perspective during retrieval of events encoded from an OE perspective, which is likely to require updating of internal representations of the world in order to retrieve memories from a novel self-location in space, and may lead to the increased functional connectivity between the hippocampus and precuneus (Chapter Two). Further, I found that the precuneus did not contain representations of visual perspective during the retrieval of memories encoded from OE and OB perspectives (Chapter Three). In this study, OB perspectives did not require participants to update the spatial layout of a mental scene, since memories were encoded and retrieved from the same perspective. Consequently, adoption of OB perspectives during memory retrieval did not impose greater demands on mental transformation processes, which may explain why visual perspective was not represented within the precuneus in this study. Consistent with this idea, precuneus activity has been associated with shifting between visual perspectives, whether shifting to an OE or OB perspective (St. Jacques et al, 2018).

Second, I found that posterior cingulate cortex contained information related to visual perspective and the interaction between visual perspective and sense of embodiment during memory retrieval (Chapter Three). Posterior cingulate cortex has previously been implicated in a number of processes including self-evaluative processing (for review see Leech & Sharp, 2013) self-referential judgments (D'Argembeau et al., 2008; D'Argembeau et al., 2005; Davey, Pujol, & Harrison, 2016), AM retrieval (Northoff & Bermpohl, 2004), and bodily self-consciousness (Guterstam, Björnsdotter, Gentile, & Ehrsson, 2015). Here, I show for the first time

that posterior cingulate cortex integrates two key components of selfhood within memories: 1) sense of embodiment (Blanke, 2012) and 2) visual perspective (Legrand & Ruby, 2009), offering new insights into the type of self-referential information processed in this region.

Third, the angular gyrus was also found to represent visual perspective according to level of embodiment, yielding new insights on the nature of multisensory, egocentric representations contained in this region. Previous investigations have shown that the patterns of activity in the angular gyrus integrate audio and visual information during memory retrieval (e.g. Bonnici, Richter, Yazar, & Simons, 2016). Chapter Four builds upon this research to show that this region is also implicated in the multisensory integration of visual signals relating to perspective and internal signals signifying sense of bodily self. Thus, sense of bodily self becomes integrated within a specific visual perspective during memory retrieval in the angular gyrus, which dovetails with findings of common recruitment of this region in studies of both AM and bodily self-consciousness (Bréchet, Grivaz, Gauthier, & Blanke, 2018). Further, this research refines the conception of egocentric representations within the angular gyrus by demonstrating that this region is sensitive to distinctions between events encoded from OE and OB perspectives according to sense of embodiment during memory retrieval. Preceding studies have shown that the angular gyrus is necessary for integrating multimodal memory features into a cohesive OE perspective; disrupting activity in this region through brain damage (Ciaramelli et al., 2010; Ionta et al., 2011), seizures (Blanke et al., 2004), or transcranial magnetic stimulation (Ciaramelli et

al., 2010; Bonnici et al., 2018; Bonnici et al., 2016; Yazar et al., 2017) impairs the ability to form OE perspectives. However, my findings imply that the mechanism enabling the angular gyrus to establish a unified OE perspective in memory is dependent upon an ability to distinguish between different visual perspectives characterized by level of embodiment. The representations of both types of visual perspectives, according to level of embodiment, may then allow the angular gyrus to supporting perspective shifting during memory retrieval (St. Jacques et al., 2017).

In sum, my research has contributed new insights into the role of MTL and posterior parietal regions in guiding memory retrieval. Visual perspective influenced functional connectivity of the hippocampus during AM retrieval across both phases of retrieval. Specifically, atypical OB perspectives were associated with increased functional connectivity between the hippocampus and a posterior medial network underlying the construction of mental scenes (Ranganath & Ritchey, 2012) early during retrieval, whereas OE perspectives were associated with increased hippocampal connectivity with an extended MTL network implicated in the visualization of mental scenes (e.g. Andrews-Hanna et al., 2010) during late retrieval. My findings concerning posterior parietal regions expand upon limited knowledge of how visual perspective and sense of embodiment at encoding interact to shape memory retrieval. I found that visual perspective and sense of embodiment within memories are supported by patterns of activity in posterior cingulate cortex and the angular gyrus, core regions of the memory retrieval network (Svoboda, McKinnon, & Levine, 2006). My findings also support

arguments that link activity in the precuneus to the manipulation of egocentric mental images, dependent on demands placed on spatial transformation processes (St. Jacques et al., 2018; Grol et al., 2017). Together, these findings advance understanding of how a dynamic sense of self rooted within a specific visual perspective and body becomes incorporated within memories of the personal past.

5.4 Limitations

Interpretation of the results within this thesis should be considered in light of certain limitations. In Chapter Two, I made an initial attempt to understand how adopting different types of OB perspectives may influence neural mechanisms of retrieval (i.e., directly facing oneself at either eye-level or floor-level). However, there are many other possible OB perspectives, which may be adopted dependent on certain events within a memory (McCarroll, 2018). Rice and Rubin (2011) identified reliable patterns between specific actions and the particular OB perspective adopted during memory retrieval. For example, swimming and running tend to be recalled from directly above an individual, whereas speaking in public is correlated with an OB perspective located in front of the individual. McCarroll (2018) suggests the interesting possibility that particular OB perspectives may be selected in order to provide the most amount of information on events within a memory. According to this logic, swimming tends to be recalled from directly above an individual because this vantage point affords the clearest view of the main action in the memory. Similarly, recalling oneself giving a public talk from the point

of view of an audience member allows one to see how one appeared to others during the speech. Thus, particular OB perspectives may be adopted in order to convey the most relevant information about an event (McCarroll, 2018). While Chapter Two made a first attempt at understanding how two different OB perspectives impact neural correlates of AM retrieval based on their typicality, this study did not take into account that events may be visualized from specific OB perspectives depending on content within the event. Instead, participants were asked to switch to typical and atypical OB perspectives without considering that these events may not be naturally be associated with these specific perspectives. Thus, there is a need for future studies cueing participants to adopt specific OB perspectives consistent with events in a given memory (e.g. recall swimming from an overhead, bird's eye perspective). This research can ultimately elucidate how visual perspective flexibly represents the self in memories to facilitate understanding of a past event.

The study in Chapter Three was designed in order to mimic naturally occurring out-of-body experiences wherein individuals feel separated from their physical bodies and see themselves from an embodied, third-person perspective (Brugger, 2002; Carruthers, 2015). However, interpretation of my findings is limited by the fact that out-of-body experiences also involve perceptions not included in this study. In particular, individuals commonly report abnormal vestibular sensations, such as a feeling of floating above one's physical body, that were not recreated here (Blanke, et al., 2004). Vestibular sensations can now be incorporated into out-of-body experiences induced in the lab due to recent

developments in immersive virtual reality simulators. For example, the Icaros© holds an individual in a position hovering above the ground and rotates forwards, backwards, and sideways during engagement with a virtual environment. Future research should take advantage of this new technology in order to make experimentally-induced out-of-body experiences induced in a laboratory setting as real as possible. Moreover, the events encoded in Chapter Four were emotionally neutral, whereas events that induce out-of-body experiences in the outside world tend to involve high emotional intensity (e.g. Cooper, Yuille, & Kennedy, 2002; Hackmann, Clark, & McManus, 2000). Having established foundational knowledge of the role of bodily selfhood and visual perspective in shaping memories for neutral events, the next step is to incorporate events with stronger levels of affect to better understand how emotion moderates this relationship. Ultimately, creating highly realistic out-of-body experiences can yield insights into behavioral and neural mechanisms underlying dissociative clinical disorders that have been difficult to investigate. For example, a better understanding of how high levels of anxiety provoked by social situations contribute to out-of-body experiences and subsequently influence memory can provide targets for therapeutic intervention.

My findings in Chapter Four are limited by the extent to which participants self-identified with their avatar, as my aim was to extend these results to real-world situations. I did find moderate levels of self-identification, however, the goal is to have create the feeling that the avatar is an exact stand-in for each participant within virtual environments. Recent advance in virtual reality technology have made this possible. For example, Bréchet and colleagues (2018) used a rig of 360-

degree cameras, binaural microphones, and custom software (i.e., Reality Substitution Machine, <http://Inco.epfl.ch/realism>) to project participants actual bodies within virtual environments. Use of this highly immersive technology has the capacity to increase the ecological validity of future research. A second limitation in Chapter Four is the assumption that OB perspectives necessarily involve a wider field of view on a scene during encoding and retrieval, which was shown to underlie the finding of increased spatial memory accuracy. Additional research is needed to directly test this assumption to clarify effects of visual perspective at encoding on objective memory accuracy.

5.5. Conclusion

The goal of this thesis was to develop current understanding of how visual perspective influences behavioral and neural mechanisms underlying memory formation and retrieval. In terms of behavior, I have laid the initial groundwork detailing the effect of different OB perspectives on memory phenomenology (Chapter Two), validated the concept of OB memories (Nigro & Neisser, 1983), and delineated how visual perspective at encoding shaped subjective and objective components of retrieval (Chapters Three and Four). Regarding neural mechanisms supporting visual perspective in memory, I have shown that visual perspective plays a key role in co-ordinating the timing of activity and functional connectivity in core memory retrieval networks (Chapter Two), and how bodily selfhood becomes integrated within visual perspective to structure memory representations in the posterior cingulate and angular gyrus (Chapter Four).

While my aim was to better understand how the sense of self shapes memory, findings of this thesis have implications for other constructive episodic processes involving mental imagery, including imagination, counterfactual thinking, and future episodic simulation (e.g. Addis, Pan, Vu, Laiser, & Schacter, 2009; De Brigard, Hanna, St. Jacques, & Schacter, 2018; St. Jacques, Carpenter, Szpunar & Schacter, 2018). For example, evidence that visual perspective plays a key role in reconstructing the personal past presented here implies that its effect on behavior and neural mechanisms during memory retrieval may be similar for other types of mental simulation that involve projecting oneself into the future and counterfactual scenarios. Thus, future studies investigating constructive episodic simulation should also account for visual perspective during mental imagery. Further, the ability to represent oneself from multiple visual perspectives may subsequently underlie theory of mind processes that enable flexible understanding of others (Carrington & Bailey, 2009). Last, my findings have implications for spatial memory, by offering new insights into the neural correlates that support egocentric representations within memory (Chapters Two and Three) and differences in spatial memory accuracy according to perspective (Chapter Four). Throughout these chapters I have demonstrated how self-specific processes of visual perspective and sense of bodily self becomes established through (re)constructive processes that occur during both memory formation and retrieval.

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Appendix A

Table 1. Session 1 Ratings

| | Autobiographical Memory Retrieval | | | | Control Task | |
|--------------------|-----------------------------------|-------------|-------------|-------------|-----------------------|-------------|
| | Own Eyes | | Observer | | Spatial Visualization | |
| | Typical | Atypical | Typical | Atypical | Typical | Atypical |
| Emotion | 3.68 (1.92) | 3.32 (1.79) | 3.64 (1.71) | 3.47 (1.79) | 3.59 (1.75) | 3.58 (1.75) |
| Familiarity | 4.82 (2.32) | 4.64 (2.12) | 4.67 (2.05) | 4.66 (2.05) | 4.45 (2.16) | 4.60 (1.95) |
| Last Visit | 4.25 (1.63) | 4.13 (1.51) | 3.80 (1.59) | 3.86 (1.78) | 3.90 (1.51) | 3.90 (1.63) |
| Vividness | 5.23 (1.73) | 5.32 (1.49) | 4.97 (1.49) | 5.08 (1.58) | 5.16 (1.48) | 5.19 (1.52) |

Mean (Standard Deviation)

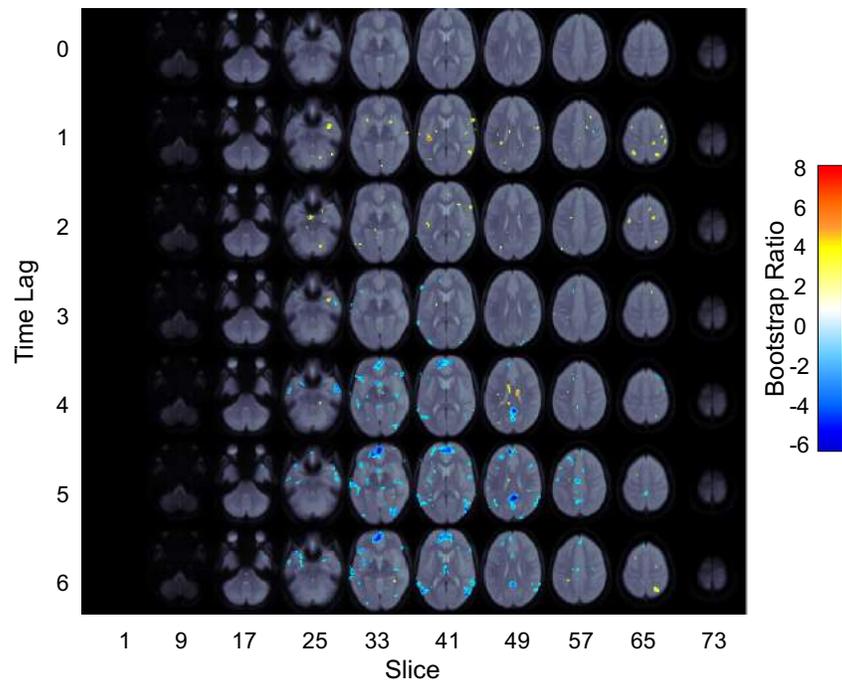


Figure 1. Spatiotemporal Task PLS Activation Time-Course. The pattern of activation extracted from the significant latent variable of the spatiotemporal PLS analysis overlaid onto a template created from averaged individual brain images. Warm colours (i.e., positive brain scores) represent activation patterns corresponding to the OE Atypical and Spatial conditions. Cool colours (i.e., negative brain scores) represent activation patterns specific to the OE Typical and OB conditions. Each time lag represents 1 TR (i.e., 2.5s). OE = Own Eyes, OB = Observer. All images depict a BSR threshold of ± 3 .

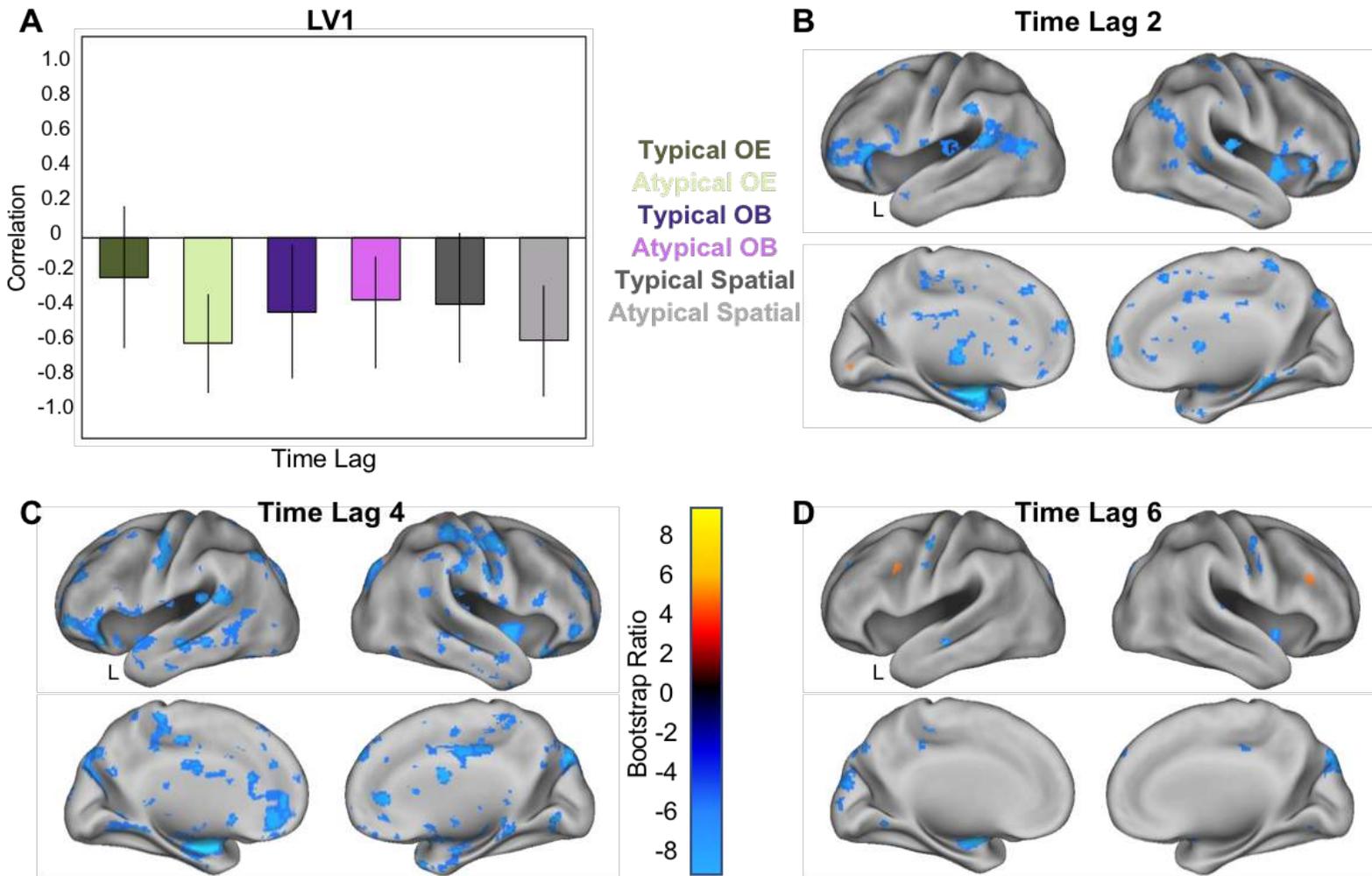


Figure 2. Hippocampus Seed PLS LV1. (A) Correlation scores associated with LV1 of the hippocampal seed PLS analysis. Error bars represent the 95% confidence interval, based on bootstrap estimates. The patterns of activation mapped onto the surface of the brain for time lags 2 (B), 4 (C), and 6 (D) are shown. OE = Own Eyes; OB = Observer. All images depict a BSR threshold of ± 3 .

Table 2. Hippocampus Seed PLS LV1

| Region | BA | x | y | z | Ratio | Cluster Size | | r | 14 | -18 | 44 | -4.53 | 162 | |
|--------------------------------------|-----|-----|-----|--------|-------|------------------------|---------------------------------|-----|-----|-----|-------|--------|-------|-----|
| | | | | | | MNI Coordinates | | | | | | | | |
| Inferior Parietal Cortex | 40 | 30 | -40 | 34 | -6.77 | 590 | | | | | | | | |
| | 39 | 52 | -60 | 34 | -4.72 | 517 | | | | | | | | |
| | 39 | 34 | -52 | 16 | -4.62 | 165 | | | | | | | | |
| | 39 | -36 | -60 | 28 | -3.54 | 114 | | | | | | | | |
| | 39 | -24 | -52 | 16 | -6.38 | 88 | | | | | | | | |
| | 39 | -38 | -78 | 38 | -3.31 | 30 | | | | | | | | |
| Negative Correlations | | | | | | | | | | | | | | |
| Dorsomedial PFC | 10 | 8 | 68 | -2 | -4.64 | 65 | | | | | | | | |
| | 8 | 8 | 12 | 42 | -5.45 | 83 | Fusiform Cortex | 37 | 40 | -66 | -18 | -4.83 | 257 | |
| | 9 | 10 | 54 | 32 | -5.46 | 64 | Visual Cortex | 19 | -46 | -68 | 12 | -5.73 | 1409 | |
| | 10 | -10 | 52 | 14 | -6.21 | 36 | | 19 | -24 | -64 | -6 | -5.21 | 108 | |
| | 8 | -12 | 36 | 38 | -4.44 | 45 | | 19 | 36 | -70 | 24 | -4.09 | 106 | |
| Lateral Frontopolar Cortex | 10 | 48 | 52 | -16 | -5.83 | 363 | | 19 | 22 | -92 | 32 | -4.43 | 45 | |
| Dorsolateral PFC | 44 | -56 | 16 | 30 | -3.88 | 35 | Thalamus | | -16 | -16 | 14 | -7.04 | 447 | |
| | 9 | 22 | 42 | 32 | -3.64 | 24 | Caudate | | -8 | 16 | -8 | -3.73 | 21 | |
| Ventrolateral PFC | 45 | -52 | 40 | 2 | -5.61 | 670 | Putamen | | -18 | 12 | 2 | -7.94 | 603 | |
| | 11 | 18 | 38 | -20 | -3.54 | 30 | | 24 | -18 | 6 | -6.78 | 490 | | |
| | 44 | -48 | 10 | 12 | -3.98 | 26 | Crus I Lobule of the Cerebellum | | -42 | -62 | -24 | -5.81 | 273 | |
| Supplementary Motor Area | 6 | 8 | 12 | 60 | -4.26 | 176 | Cerebellum Lobule IV, V | | 10 | -54 | -6 | -4.22 | 39 | |
| | 6 | -16 | -22 | 66 | -4.96 | 93 | | 10 | -52 | -22 | -3.61 | 26 | | |
| | 6 | 6 | -22 | 62 | -4.33 | 57 | Cerebellum Lobule VI | | -34 | -36 | -28 | -3.69 | 29 | |
| Anterior Premotor Cortex | 8 | -32 | 20 | 40 | -5.24 | 452 | | 40 | -38 | -32 | -3.83 | 49 | | |
| | 8 | 36 | 14 | 52 | -6.20 | 261 | Vermis | | -2 | -56 | -2 | -3.69 | 23 | |
| | 8 | -20 | 26 | 28 | -3.82 | 27 | | 2 | -68 | -24 | -7.11 | 1051 | | |
| Motor Cortex | 4 | 28 | -24 | 66 | -4.28 | 63 | | | | | | | | |
| Insula | 13 | 32 | 22 | -4 | -4.08 | 25 | | | | | | | | |
| Somatosensory Cortex | 1 | 26 | -40 | 36 | -5.84 | 25 | Negative Correlations | | | | | | | |
| Auditory Cortex | 41 | 40 | -20 | 12 | -4.01 | 46 | Dorsomedial PFC | 8 | -12 | 28 | 36 | -5.21 | 128 | |
| Amygdala | -28 | -6 | -18 | -5.18 | 218 | | | 10 | -10 | 66 | 14 | -3.88 | 100 | |
| | 24 | 0 | -24 | -3.87 | 70 | Ventromedial PFC | | 11 | -2 | 48 | -26 | -3.43 | 22 | |
| Superior Temporal Cortex | 22 | 70 | -24 | 2 | -5.25 | 74 | Lateral Frontopolar Cortex | | 10 | -16 | 60 | 4 | -4.89 | 627 |
| | 38 | 32 | 12 | -40 | -4.31 | 70 | | 10 | 22 | 40 | 6 | -4.37 | 70 | |
| | 38 | 56 | 18 | -14 | -4.39 | 39 | | 10 | -14 | 50 | 4 | -4.35 | 31 | |
| | 38 | 42 | 8 | -24 | -3.83 | 22 | Dorsolateral PFC | 9 | 34 | 44 | 26 | -4.46 | 67 | |
| Middle Temporal Cortex | -10 | -60 | -38 | -8 | -5.35 | 245 | | 9 | -30 | 20 | 40 | -3.78 | 30 | |
| | 21 | 68 | -38 | -6 | -4.80 | 183 | Ventrolateral PFC | 44 | -58 | 20 | 26 | -4.78 | 147 | |
| | 21 | 46 | -44 | 2 | -4.80 | 49 | Anterior Cingulate Cortex | 32 | 4 | 42 | 8 | -3.62 | 66 | |
| Inferior Temporal Cortex | 20 | -32 | -4 | -42 | -4.44 | 63 | Supplementary Motor Area | 6 | 12 | 26 | 54 | -3.81 | 74 | |
| Middle Cingulate Cortex | 24 | -10 | 6 | 34 | -4.15 | 43 | Anterior Premotor Cortex | 8 | -32 | 28 | 52 | -4.31 | 218 | |
| Posterior Cingulate | 31 | -10 | -38 | 52 | -4.82 | 147 | | 8 | -14 | 32 | 22 | -4.34 | 83 | |
| | 23 | 14 | -44 | 34 | -4.85 | 41 | | 8 | 32 | 16 | 32 | -4.19 | 36 | |
| | 23 | -2 | -40 | 32 | -4.83 | 27 | Premotor Cortex | 6 | -34 | 4 | 44 | -4.75 | 50 | |
| Precuneus | 7 | -8 | -46 | 70 | -5.32 | 66 | Motor Cortex | 4 | -50 | -12 | 50 | -6.27 | 536 | |
| Somatosensory Cortex | 1 | 32 | -30 | 48 | -4.13 | 48 | | 4 | -64 | -6 | 24 | -3.67 | 36 | |
| Superior Parietal Cortex | 7 | -32 | -44 | 48 | -3.47 | 21 | Amygdala | 53 | -26 | -4 | -20 | -14.35 | 13743 | |
| Inferior Parietal Cortex | 39 | -36 | -60 | 48 | -5.13 | 191 | Insula | 13 | 32 | -20 | 16 | -9.52 | 10728 | |
| | 39 | -50 | -66 | 14 | -4.30 | 103 | | 13 | 48 | 6 | -8 | -7.44 | 4563 | |
| | 39 | 52 | -50 | 20 | -4.75 | 97 | Superior Temporal Cortex | 38 | -54 | 6 | -28 | -4.12 | 36 | |
| | 39 | 42 | -64 | 42 | -3.80 | 35 | Middle Temporal Cortex | 21 | -70 | -20 | -16 | -3.70 | 24 | |
| Visual Cortex | 40 | -50 | -42 | 46 | -3.61 | 30 | Superior Parietal Cortex | 7 | -34 | -74 | 52 | -5.29 | 303 | |
| | 18 | 30 | -92 | 8 | -5.12 | 107 | | 40 | 50 | -46 | 56 | -5.38 | 127 | |
| | 18 | 38 | -84 | -2 | -4.18 | 54 | | 7 | 34 | -64 | 56 | -3.89 | 110 | |
| | 18 | -26 | -98 | 10 | -4.51 | 29 | Inferior Parietal Cortex | 39 | 46 | -66 | 40 | -3.98 | 39 | |
| Thalamus | -8 | -8 | -12 | 2 | -4.46 | 50 | | 39 | -36 | 50 | 32 | -4.15 | 34 | |
| Caudate | 16 | 6 | 12 | -5.50 | 286 | | 39 | -48 | -52 | 40 | -3.55 | 26 | | |
| | -20 | -12 | 20 | -4.14 | 27 | Visual Cortex | 40 | -46 | -28 | 28 | -4.15 | 22 | | |
| Putamen | -20 | 8 | 2 | -6.60 | 269 | | 19 | 16 | -78 | 40 | -6.75 | 1906 | | |
| Crus I Lobule of the Cerebellum | -16 | 14 | -10 | -3.79 | 44 | | 18 | 10 | -76 | -2 | -4.23 | 59 | | |
| Cerebellum Lobule IV, V | -22 | -86 | -24 | -3.68 | 27 | | 18 | 20 | -52 | 6 | -3.49 | 46 | | |
| Cerebellum Lobule VI | 16 | -48 | -22 | -5.14 | 56 | | 19 | -28 | -86 | 16 | -4.15 | 41 | | |
| | 10 | -70 | -22 | -4.42 | 34 | Vermis | | -2 | -72 | -24 | -6.90 | 1114 | | |
| | | | | | | | | | | | | | | |
| Positive Correlations | | | | | | | | | | | | | | |
| Visual Cortex | 18 | -8 | -90 | -6 | 4.02 | 22 | Negative Correlations | | | | | | | |
| | | | | | | | Dorsomedial PFC | 8 | -4 | 36 | 40 | -3.88 | 71 | |
| Negative Correlations | | | | | | | | 9 | 10 | 40 | 32 | -3.92 | 38 | |
| Dorsomedial PFC | 10 | -8 | 64 | 14 | -6.47 | 399 | Dorsolateral PFC | 9 | 20 | 54 | 34 | -6.29 | 927 | |
| | 10 | 10 | 66 | 8 | -7.95 | 361 | Ventrolateral PFC | 46 | -32 | 42 | 2 | -7.50 | 4107 | |
| | 8 | -8 | 32 | 42 | -4.76 | 154 | | 47 | -44 | 24 | -14 | -7.59 | 1475 | |
| Lateral Frontopolar Cortex | 9 | 8 | 54 | 32 | -3.69 | 23 | Anterior Premotor Cortex | 44 | -56 | 18 | 28 | -4.90 | 95 | |
| | 10 | 44 | 48 | -12 | -6.98 | 686 | Premotor Cortex | 8 | 32 | 18 | 48 | -4.75 | 101 | |
| | 10 | -28 | 38 | 22 | -3.86 | 134 | | 6 | -22 | 28 | 58 | -4.69 | 328 | |
| Dorsolateral PFC | 9 | 30 | 42 | 26 | -3.96 | 59 | Thalamus | 6 | -16 | -22 | 44 | -5.56 | 142 | |
| Ventrolateral PFC | 45 | 50 | 24 | 0 | -6.17 | 2490 | | 6 | -10 | 42 | 28 | -4.29 | 39 | |
| | 47 | -36 | 28 | -8 | -6.46 | 2085 | Motor Cortex | 6 | -36 | 8 | 56 | -4.42 | 31 | |
| Supplementary Motor Area | 44 | 62 | 22 | 12 | -4.12 | 104 | Amygdala | 4 | -46 | -12 | 44 | -5.95 | 575 | |
| Anterior Premotor Cortex | 6 | -2 | -12 | 60 | -3.64 | 31 | | 53 | -24 | -6 | -20 | -19.68 | 12692 | |
| | 8 | 36 | 8 | 58 | -4.38 | 171 | Auditory Cortex | 41 | 68 | 0 | 2 | -4.70 | 44 | |
| | 8 | 38 | 24 | 38 | -4.27 | 150 | Somatosensory Cortex | 1 | 32 | -32 | 56 | -6.94 | 3296 | |
| Premotor Cortex | 6 | -18 | 24 | 60 | -4.01 | 80 | Precuneus | 7 | -6 | -58 | 68 | -4.11 | 62 | |
| | 6 | -14 | -2 | 44 | -5.53 | 78 | Inferior Parietal Cortex | 39 | -60 | -48 | 18 | -5.61 | 290 | |
| | 6 | -22 | 10 | 64 | -3.62 | 28 | Fusiform Cortex | 39 | 44 | -50 | 22 | -4.57 | 157 | |
| | 6 | -38 | 2 | 46 | -3.75 | 21 | | 37 | 38 | -54 | -18 | -4.16 | 210 | |
| Motor Cortex | 4 | 38 | -16 | 40 | -4.54 | 130 | Visual Cortex | 37 | 62 | -40 | -18 | -3.69 | 57 | |
| | 4 | -44 | -14 | 46 | -4.57 | 110 | | 37 | -30 | -34 | -26 | -3.94 | 41 | |
| Somatosensory Cortex | 1 | 50 | -10 | 18 | -4.77 | 34 | | 18 | -28 | -56 | 22 | -8.08 | 4865 | |
| Hippocampus | -28 | -6 | -22 | -14.24 | 1398 | | 19 | 16 | -82 | 40 | -6.20 | 2693 | | |
| Perirhinal Cortex | 36 | 24 | -4 | -36 | -4.78 | 28 | | 18 | 12 | -74 | 0 | -5.21 | 753 | |
| Posterior Parietophippocampal Cortex | 36 | 16 | -34 | -14 | -8.84 | 587 | | 18 | -10 | -98 | 18 | -4.11 | 77 | |
| Auditory Cortex | 41 | -44 | -30 | 6 | -5.83 | 252 | Caudate | 19 | -40 | -80 | 4 | -3.93 | 37 | |
| | 41 | 66 | -16 | 6 | -4.39 | 104 | Putamen | 19 | -4 | 10 | 10 | -4.02 | 29 | |
| | 41 | 70 | -24 | 14 | -4.70 | 66 | Thalamus | -22 | -2 | 4 | 4 | -4.05 | 51 | |
| | 41 | 52 | -10 | -2 | -4.77 | 39 | | 0 | -6 | 0 | -4.58 | 76 | | |
| Superior Temporal Cortex | 22 | 62 | -38 | 8 | -4.66 | 471 | Crus I Lobule of the Cerebellum | -30 | -76 | -32 | -4.10 | 58 | | |
| | 22 | -48 | 2 | -12 | -4.17 | 191 | Cerebellum Lobule VI | -38 | -60 | -22 | -5.01 | 147 | | |
| Middle Temporal Cortex | 38 | 34 | 18 | -36 | -5.65 | 45 | | | | | | | | |
| Inferior Temporal Cortex | 21 | 72 | -14 | -18 | -4.30 | 33 | Positive Correlations | | | | | | | |
| Anterior Cingulate Cortex | 32 | 8 | 10 | 40 | -4.21 | 177 | Premotor Cortex | 6 | -38 | 4 | 28 | 3.85 | 55 | |
| | 32 | 6 | 40 | -4 | -3.60 | 26 | Supramarginal Cortex | 40 | -46 | -36 | 36 | 4.03 | 25 | |
| Posterior Cingulate Cortex | 31 | -8 | -38 | 50 | -4.98 | 409 | Superior Parietal Cortex | 7 | -24 | -62 | 56 | 4.01 | 24 | |
| | 23 | -12 | -34 | 30 | -5.90 | 340 | Inferior Parietal Cortex | 39 | 24 | -58 | 40 | 3.82 | 25 | |
| | 31 | 2 | -24 | 40 | -3.67 | 38 | | | | | | | | |
| Somatosensory Cortex | 23 | 8 | -52 | 16 | -3.76 | 26 | Negative Correlations | | | | | | | |
| Precuneus | 1 | -18 | -34 | 66 | -4.71 | 314 | Ventromedial PFC | 11 | 4 | 66 | -16 | -5.06 | 181 | |

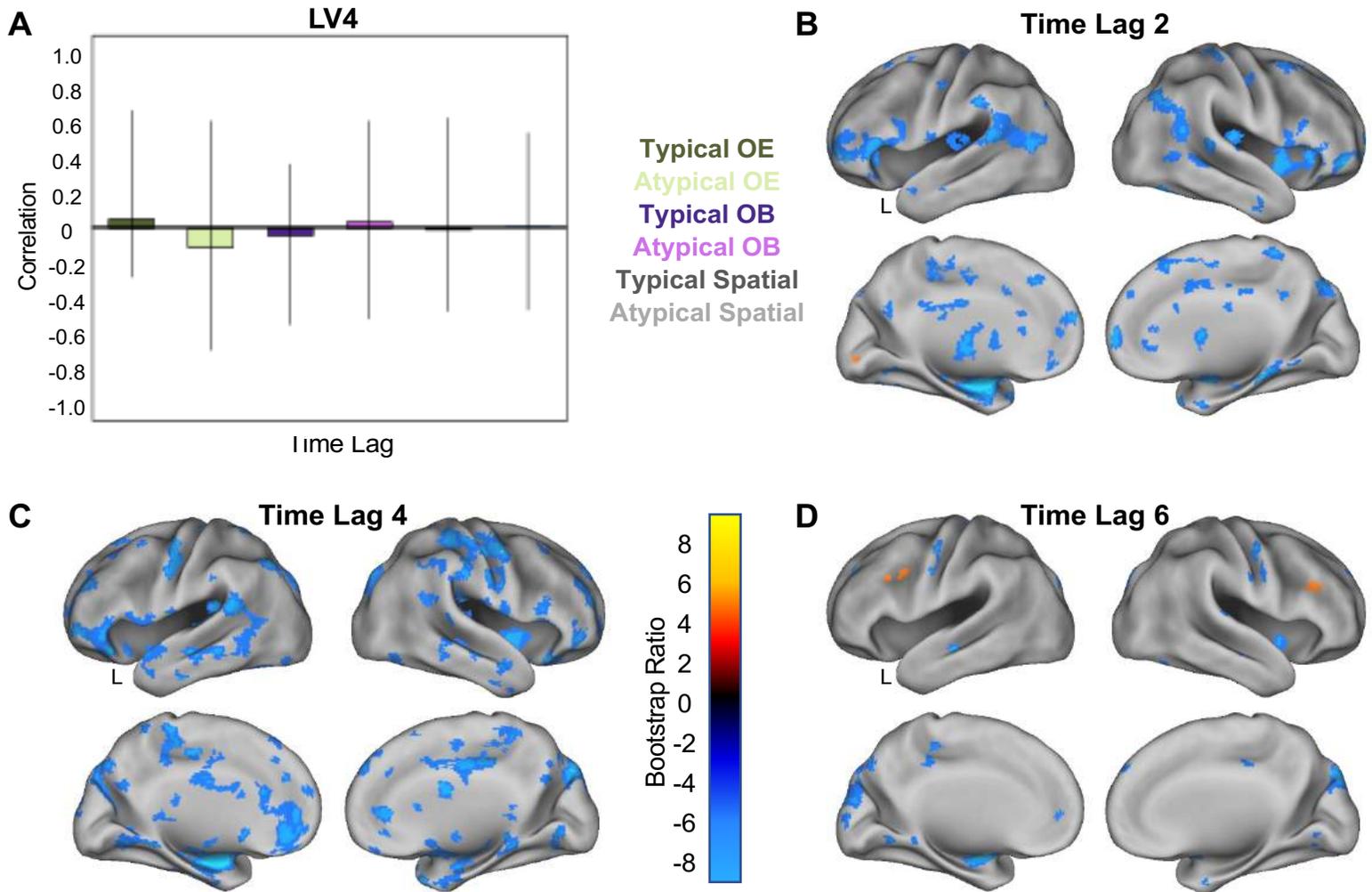


Figure 3. Hippocampal Seed PLS LV4. (A) Correlation scores associated with LV4 of the hippocampal seed PLS analysis. Error bars represent the 95% confidence interval, based on bootstrap estimates. The patterns of activation mapped onto the surface of the brain from times lags 2 (B), 4 (C), and 6 (D) are shown. All images depict a BSR threshold of ± 3 .

Table 3. Hippocampus Seed PLS LV4 Activations

| Region | BA | MNI Coordinates | | | Ratio | Cluster Size | Time Lag 3 | | | | | | | | | |
|---------------------------------|------------|---------------------------------|-----|-----|-------|--------------|-----------------------|------|------------------------------|-------|-------|--------|--------|-------|--|--|
| | | x | y | z | | | Negative Correlations | | | | | | | | | |
| Negative Correlations | Time Lag 1 | Dorsomedial PFC | 8 | -12 | 36 | 38 | -4.44 | 45 | 8 | -12 | 28 | 36 | -5.21 | 128 | | |
| | | Dorsomedial PFC | 10 | -10 | 52 | 14 | -6.21 | 36 | 10 | -10 | 66 | 14 | -3.88 | 100 | | |
| | | Dorsomedial PFC | 8 | 8 | 12 | 42 | -5.45 | 73 | 11 | -2 | 48 | -26 | -3.43 | 22 | | |
| | | Dorsomedial PFC | 10 | 8 | 68 | -2 | -4.64 | 65 | 10 | -16 | 60 | 4 | -4.89 | 627 | | |
| | | Dorsomedial PFC | 9 | 10 | 54 | 32 | -5.46 | 64 | 20 | -14 | 50 | 4 | -4.35 | 31 | | |
| | | Dorsomedial PFC | 11 | 18 | 38 | -20 | -3.54 | 30 | 9 | 34 | 44 | 26 | -4.46 | 67 | | |
| | | Dorsomedial PFC | 10 | 48 | 52 | -16 | -5.83 | 363 | 6 | 12 | 26 | 54 | -3.81 | 74 | | |
| | | Dorsomedial PFC | 10 | 24 | 60 | -14 | -4.44 | 20 | 44 | -58 | 20 | 26 | -4.78 | 147 | | |
| | | Dorsomedial PFC | 9 | 22 | 42 | 32 | -3.64 | 24 | 8 | -32 | 28 | 52 | -4.31 | 218 | | |
| | | Dorsomedial PFC | 44 | -56 | 16 | 30 | -3.88 | 35 | 8 | 32 | 16 | 32 | -4.19 | 36 | | |
| Ventromedial PFC | Time Lag 1 | Ventromedial PFC | 10 | 48 | 52 | -16 | -5.83 | 363 | 6 | -34 | 4 | 44 | -4.75 | 39 | | |
| | | Ventromedial PFC | 10 | 24 | 60 | -14 | -4.44 | 20 | 4 | -50 | -12 | 50 | -6.27 | 536 | | |
| | | Ventromedial PFC | 44 | -56 | 16 | 30 | -3.88 | 35 | 4 | -64 | -6 | 24 | -3.67 | 36 | | |
| | | Ventromedial PFC | 44 | -48 | 10 | 12 | -3.98 | 26 | 32 | 4 | 42 | 8 | -3.62 | 66 | | |
| | | Ventromedial PFC | 6 | 8 | 12 | 60 | -4.26 | 176 | 13 | 32 | -20 | 16 | -9.52 | 10728 | | |
| | | Ventromedial PFC | 6 | 6 | -22 | 62 | -4.53 | 67 | 13 | 48 | 6 | -8 | -7.44 | 4563 | | |
| | | Ventromedial PFC | 8 | 36 | 14 | 52 | -6.20 | 261 | 13 | -26 | -4 | -20 | -14.35 | 13743 | | |
| | | Ventromedial PFC | 8 | -32 | 20 | 40 | -5.24 | 452 | 38 | -54 | 6 | -28 | -4.12 | 36 | | |
| | | Ventromedial PFC | 8 | 36 | 14 | 52 | -6.20 | 261 | 21 | -70 | -20 | -16 | -3.70 | 24 | | |
| | | Ventromedial PFC | 6 | -16 | -22 | 66 | -4.96 | 93 | 7 | -34 | -74 | 52 | -5.29 | 303 | | |
| Supplementary Motor Area | Time Lag 1 | Supplementary Motor Area | 13 | 32 | 22 | -4 | -4.08 | 25 | 34 | -64 | 56 | -3.89 | 110 | | | |
| | | Supplementary Motor Area | 8 | -32 | 20 | 40 | -5.24 | 452 | 40 | -36 | -50 | 32 | -4.15 | 34 | | |
| | | Supplementary Motor Area | 8 | 36 | 14 | 52 | -6.20 | 261 | 39 | -48 | -52 | 40 | -3.55 | 26 | | |
| | | Supplementary Motor Area | 6 | -16 | -22 | 66 | -4.96 | 93 | 40 | -46 | -28 | 28 | -4.15 | 22 | | |
| | | Supplementary Motor Area | 4 | 28 | -24 | 66 | -4.28 | 63 | 39 | 24 | -44 | 34 | -8.84 | 2945 | | |
| | | Supplementary Motor Area | 13 | 32 | 22 | -4 | -4.08 | 25 | 40 | 50 | -46 | 56 | -5.38 | 127 | | |
| | | Supplementary Motor Area | 38 | 56 | 18 | -14 | -4.39 | 39 | 39 | 46 | -66 | 40 | -3.98 | 39 | | |
| | | Supplementary Motor Area | 38 | 42 | 8 | -24 | -3.83 | 22 | 19 | -28 | -86 | 16 | -4.15 | 41 | | |
| | | Supplementary Motor Area | 21 | -60 | -38 | -8 | -5.35 | 245 | 19 | 16 | -78 | 40 | -6.75 | 1906 | | |
| | | Supplementary Motor Area | 21 | 68 | -38 | -6 | -4.80 | 183 | 18 | 10 | -76 | -2 | -4.23 | 59 | | |
| Premotor Cortex | Time Lag 1 | Premotor Cortex | 20 | -32 | -4 | -4.42 | 147 | 18 | 20 | -52 | 6 | -3.49 | 46 | | | |
| | | Premotor Cortex | 23 | -2 | -40 | 32 | -4.83 | 27 | -2 | -72 | -24 | -6.90 | 1114 | | | |
| | | Premotor Cortex | 23 | 14 | -44 | 34 | -4.85 | 41 | Negative Correlations | | | | | | | |
| | | Premotor Cortex | 7 | -8 | -46 | 70 | -5.32 | 66 | 8 | -4 | 36 | 40 | -3.88 | 71 | | |
| | | Premotor Cortex | 1 | 32 | -30 | 48 | -4.13 | 21 | 9 | 10 | 40 | 32 | -3.92 | 38 | | |
| | | Premotor Cortex | 7 | -32 | -44 | 48 | -4.47 | 21 | 44 | -56 | 18 | 28 | -4.90 | 95 | | |
| | | Premotor Cortex | 39 | -36 | -60 | 48 | -5.13 | 191 | 9 | -10 | 42 | 28 | -4.29 | 39 | | |
| | | Premotor Cortex | 39 | -50 | -66 | 14 | -4.30 | 103 | 9 | 20 | 54 | 34 | -6.29 | 927 | | |
| | | Premotor Cortex | 40 | -50 | -66 | 14 | -4.30 | 103 | 46 | -32 | 42 | 2 | -7.50 | 4107 | | |
| | | Premotor Cortex | 40 | -50 | -66 | 14 | -4.30 | 103 | 47 | -44 | 24 | -14 | -7.59 | 1475 | | |
| Visual Cortex | Time Lag 1 | Visual Cortex | 39 | 52 | -50 | 20 | -4.75 | 97 | 8 | 32 | 18 | 48 | -4.75 | 101 | | |
| | | Visual Cortex | 39 | 42 | -64 | 42 | -3.80 | 35 | 6 | -22 | 28 | 58 | -4.69 | 328 | | |
| | | Visual Cortex | 18 | -26 | -98 | 10 | -4.51 | 29 | 6 | -16 | -22 | 44 | -5.56 | 142 | | |
| | | Visual Cortex | 18 | 30 | -92 | 8 | -5.12 | 107 | 6 | -36 | 8 | 56 | -4.42 | 31 | | |
| | | Visual Cortex | 18 | 38 | -84 | -2 | -4.18 | 54 | 4 | -46 | -12 | 44 | -5.95 | 575 | | |
| | | Visual Cortex | 16 | 8 | 12 | -5.50 | 286 | 4 | -24 | -6 | -20 | -19.68 | 12692 | | | |
| | | Visual Cortex | 22 | 68 | 0 | 2 | -4.70 | 44 | 22 | 68 | 0 | 2 | -4.70 | 44 | | |
| | | Visual Cortex | 1 | 32 | -32 | 56 | -6.34 | 3296 | 1 | -6 | -58 | 68 | -4.11 | 62 | | |
| | | Visual Cortex | 39 | -28 | -56 | 22 | -8.08 | 4865 | 39 | -60 | -48 | 18 | -5.61 | 290 | | |
| | | Visual Cortex | 39 | 44 | -50 | 22 | -4.57 | 157 | 39 | -60 | -48 | 18 | -5.61 | 290 | | |
| Caudate | Time Lag 1 | Caudate | 18 | 30 | -92 | 8 | -5.12 | 107 | 37 | -30 | -34 | -26 | -3.94 | 41 | | |
| | | Caudate | 37 | 38 | -54 | -18 | -4.16 | 210 | 37 | 38 | -54 | -18 | -4.16 | 210 | | |
| | | Caudate | 37 | 62 | -40 | -18 | -3.69 | 57 | 18 | -10 | -98 | 18 | -4.11 | 77 | | |
| | | Caudate | 19 | -40 | -84 | -14 | -3.67 | 37 | 19 | -40 | -84 | -14 | -3.67 | 37 | | |
| | | Caudate | 19 | -48 | -80 | 4 | -3.93 | 29 | 19 | 16 | -82 | 40 | -6.20 | 2693 | | |
| | | Caudate | 18 | 12 | -74 | 0 | -5.21 | 753 | 14 | 4 | 10 | -4.02 | 26 | | | |
| | | Caudate | 14 | 4 | 10 | -4.02 | 26 | 14 | 4 | 10 | -4.02 | 26 | | | | |
| | | Caudate | 14 | 4 | 10 | -4.02 | 26 | 14 | 4 | 10 | -4.02 | 26 | | | | |
| | | Caudate | 14 | 4 | 10 | -4.02 | 26 | 14 | 4 | 10 | -4.02 | 26 | | | | |
| | | Caudate | 14 | 4 | 10 | -4.02 | 26 | 14 | 4 | 10 | -4.02 | 26 | | | | |
| Putamen | Time Lag 1 | Putamen | -20 | 8 | 2 | -6.80 | 269 | 14 | 4 | 10 | -4.02 | 26 | | | | |
| | | Putamen | -16 | 14 | -10 | -3.79 | 44 | 14 | 4 | 10 | -4.02 | 26 | | | | |
| | | Putamen | 8 | -12 | 2 | -4.46 | 50 | 14 | 4 | 10 | -4.02 | 26 | | | | |
| | | Putamen | 8 | -6 | 6 | -4.39 | 20 | 14 | 4 | 10 | -4.02 | 26 | | | | |
| | | Putamen | -22 | -86 | -24 | -3.68 | 27 | 14 | 4 | 10 | -4.02 | 26 | | | | |
| | | Putamen | -10 | -40 | -5.68 | 113 | 14 | 4 | 10 | -4.02 | 26 | | | | | |
| | | Putamen | 16 | -48 | -22 | -5.14 | 56 | 14 | 4 | 10 | -4.02 | 26 | | | | |
| | | Putamen | 10 | -70 | -22 | -4.42 | 34 | 14 | 4 | 10 | -4.02 | 26 | | | | |
| | | Putamen | 10 | -70 | -22 | -4.42 | 34 | 14 | 4 | 10 | -4.02 | 26 | | | | |
| | | Putamen | 10 | -70 | -22 | -4.42 | 34 | 14 | 4 | 10 | -4.02 | 26 | | | | |
| Crus 1 Lobule of the Cerebellum | Time Lag 1 | Crus 1 Lobule of the Cerebellum | 10 | -8 | 64 | 14 | -6.47 | 399 | 10 | -8 | 64 | 14 | -6.47 | 399 | | |
| | | Crus 1 Lobule of the Cerebellum | 8 | -8 | 32 | 42 | -4.76 | 154 | 10 | 10 | 66 | 8 | -7.95 | 361 | | |
| | | Crus 1 Lobule of the Cerebellum | 10 | 10 | 66 | 8 | -7.95 | 361 | 9 | 8 | 54 | 32 | -3.69 | 23 | | |
| | | Crus 1 Lobule of the Cerebellum | 9 | 8 | 54 | 32 | -3.69 | 23 | 10 | -28 | 38 | -22 | -3.86 | 134 | | |
| | | Crus 1 Lobule of the Cerebellum | 10 | 44 | 48 | 12 | -6.98 | 686 | 10 | 44 | 48 | 12 | -6.98 | 686 | | |
| | | Crus 1 Lobule of the Cerebellum | 9 | 30 | 42 | 6 | -3.96 | 59 | 9 | 30 | 42 | 6 | -3.96 | 59 | | |
| | | Crus 1 Lobule of the Cerebellum | 47 | -36 | 28 | -8 | -6.46 | 2085 | 45 | -12 | -34 | 30 | -5.90 | 340 | | |
| | | Crus 1 Lobule of the Cerebellum | 45 | -12 | -34 | 30 | -5.90 | 340 | 45 | 50 | 24 | 0 | -6.17 | 2490 | | |
| | | Crus 1 Lobule of the Cerebellum | 6 | -2 | -12 | 60 | -3.64 | 31 | 6 | -2 | -12 | 60 | -3.64 | 31 | | |
| | | Crus 1 Lobule of the Cerebellum | 62 | 22 | -12 | -4.12 | 104 | 62 | 22 | -12 | -4.12 | 104 | | | | |
| Cerebellum Lobule III | Time Lag 1 | Cerebellum Lobule III | 8 | -30 | 20 | 40 | -4.53 | 91 | 10 | -12 | 50 | 2 | -6.79 | 705 | | |
| | | Cerebellum Lobule III | 8 | 36 | 8 | 58 | -4.38 | 171 | 8 | -4 | 38 | 56 | -3.54 | 23 | | |
| | | Cerebellum Lobule III | 8 | 38 | 24 | 38 | -4.27 | 150 | 9 | 8 | 60 | 32 | -5.92 | 305 | | |
| | | Cerebellum Lobule III | 6 | -18 | 24 | 60 | -4.01 | 80 | 10 | -2 | 48 | -10 | -4.32 | 133 | | |
| | | Cerebellum Lobule III | 6 | -14 | -2 | 44 | -5.53 | 78 | 11 | -10 | 16 | -12 | -4.79 | 98 | | |
| | | Cerebellum Lobule III | 6 | -22 | 10 | 64 | -3.62 | 28 | 11 | 4 | 66 | 4 | -5.06 | 181 | | |
| | | Cerebellum Lobule III | 6 | -38 | 2 | 46 | -3.75 | 21 | 10 | 20 | 58 | 4 | -7.11 | 258 | | |
| | | Cerebellum Lobule III | 4 | -44 | -14 | 46 | -4.57 | 103 | 9 | -22 | 42 | 34 | -4.94 | 157 | | |
| | | Cerebellum Lobule III | 4 | -44 | -14 | 46 | -4.57 | 103 | 47 | -56 | 34 | -8 | -4.78 | 342 | | |
| | | Cerebellum Lobule III | 4 | -44 | -14 | 46 | -4.57 | 103 | 47 | -56 | 34 | -8 | -4.78 | 342 | | |
| Cerebellum Lobule IV, V | Time Lag 1 | Cerebellum Lobule IV, V | 41 | -44 | -30 | 6 | -5.83 | 252 | 47 | 18 | 42 | -12 | -3.80 | 51 | | |
| | | Cerebellum Lobule IV, V | 41 | 66 | -16 | 6 | -4.39 | 104 | 8 | -16 | 48 | 44 | -3.71 | 26 | | |
| | | Cerebellum Lobule IV, V | 41 | 52 | -10 | -2 | -4.77 | 39 | 8 | -32 | 20 | 44 | -4.16 | 30 | | |
| | | Cerebellum Lobule IV, V | 41 | 52 | -10 | -2 | -4.77 | 39 | 6 | -20 | 26 | 56 | -6.60 | 390 | | |
| | | Cerebellum Lobule IV, V | 6 | 50 | -12 | 50 | -5.16 | 155 | 6 | 52 | -4 | 36 | -3.77 | 39 | | |
| | | Cerebellum Lobule IV, V | 6 | 52 | -4 | 36 | -3.77 | 39 | 4 | -54 | -10 | 36 | -5.72 | 244 | | |
| | | Cerebellum Lobule IV, V | 4 | -14 | -2 | 44 | -5.53 | 78 | 4 | -38 | -10 | 28 | -5.56 | 85 | | |
| | | Cerebellum Lobule IV, V | 4 | -14 | -2 | 44 | -5.53 | 78 | 13 | 48 | 10 | 2 | -4.43 | 21 | | |
| | | Cerebellum Lobule IV, V | 41 | 66 | -16 | 6 | -4.39 | 104 | 41 | 72 | -24 | 10 | -5.42 | 469 | | |
| | | Cerebellum Lobule IV, V | 41 | 52 | -10 | -2 | -4.77 | 39 | 41 | 38 | -30 | 8 | -4.84 | 36 | | |
| Cerebellum Lobule VI | Time Lag 1 | Cerebellum Lobule VI | 36 | 24 | -4 | -7.78 | 36 | 38 | -56 | -6 | -20 | -18.24 | 2147 | | | |
| | | Cerebellum Lobule VI | 36 | 16 | -34 | -14 | -8.84 | 587 | 38 | -52 | 6 | -30 | -3.75 | 21 | | |
| | | Cerebellum Lobule VI | 22 | 62 | -38 | 8 | -4.66 | 471 | 20 | 54 | -4 | -38 | -4.66 | 158 | | |
| | | Cerebellum Lobule VI | 22 | -48 | 2 | -12 | -4.17 | 191 | | | | | | | | |

| | Time Lag 6 | | | | | |
|----------------------------------|------------|-----|-----|-----|-------|------|
| Positive Correlations | | | | | | |
| Dorsolateral PFC | 9 | -40 | 22 | 30 | 4.17 | 50 |
| | 9 | 48 | 26 | 24 | 3.51 | 37 |
| Premotor Cortex | 6 | -26 | 2 | 38 | 5.47 | 157 |
| | 6 | 22 | 2 | 44 | 4.27 | 97 |
| | 6 | 16 | 16 | 52 | 3.63 | 30 |
| Superior Parietal Cortex | 40 | -48 | -36 | 34 | 4.29 | 47 |
| Inferior Parietal Cortex | 39 | 26 | -58 | 42 | 3.72 | 21 |
| Fusiform Cortex | 37 | -40 | -80 | -8 | 4.33 | 67 |
| Visual Cortex | 18 | 24 | -94 | 2 | 3.63 | 20 |
| Caudate | | -16 | 10 | 14 | 3.54 | 72 |
| Negative Correlations | | | | | | |
| Dorsomedial PFC | 10 | 2 | 68 | -12 | -3.86 | 60 |
| Lateral Frontopolar Cortex | 10 | -14 | 48 | 2 | -5.14 | 127 |
| Dorsolateral PFC | 9 | -24 | 42 | 32 | -4.54 | 21 |
| Dorsolateral PFC | 9 | 18 | 54 | 34 | -4.05 | 111 |
| Ventrolateral PFC | 44 | 62 | 22 | 6 | -3.79 | 22 |
| Premotor Cortex | 6 | -24 | -20 | 64 | -4.44 | 132 |
| | 6 | 50 | -10 | 50 | -5.09 | 156 |
| | 6 | 28 | -8 | 32 | -6.61 | 102 |
| Motor Cortex | 4 | -55 | -12 | 38 | -5.47 | 142 |
| Insula | 13 | 42 | 6 | -10 | -4.59 | 46 |
| Auditory Cortex | 41 | 66 | -26 | 10 | -3.99 | 38 |
| | 41 | 50 | -8 | -2 | -3.66 | 22 |
| Amygdala | | -24 | -2 | -18 | -3.53 | 315 |
| | | 22 | 2 | -22 | -6.16 | 196 |
| Posterior Parahippocampal Cortex | 36 | -14 | -20 | -16 | -4.80 | 41 |
| Superior Temporal Cortex | 22 | -40 | -42 | 16 | -4.12 | 24 |
| | 22 | 42 | -24 | -4 | -4.20 | 51 |
| Middle Temporal Cortex | 21 | -54 | -20 | -12 | -5.04 | 73 |
| | 21 | 62 | -14 | -18 | -3.49 | 27 |
| | 21 | 70 | -8 | -20 | -4.90 | 30 |
| Inferior Temporal Cortex | 20 | -48 | -10 | -32 | -4.67 | 92 |
| Middle Cingulate Cortex | 24 | 0 | -4 | 42 | -3.62 | 32 |
| Posterior Cingulate Cortex | 31 | -8 | -38 | 50 | -5.29 | 185 |
| Retrosplenial Cortex | 30 | -26 | -50 | 12 | -4.99 | 252 |
| Precuneus | 7 | -8 | -80 | 68 | -4.75 | 112 |
| Superior Parietal Cortex | 7 | 12 | -82 | 46 | -5.29 | 1491 |
| | 7 | -20 | -46 | 52 | -4.51 | 20 |
| | 7 | 20 | -46 | 64 | -4.50 | 79 |
| Inferior Parietal Cortex | 40 | -48 | -34 | 16 | -5.72 | 187 |
| | 39 | 20 | -44 | 34 | -5.57 | 209 |
| Visual Cortex | 19 | -38 | -66 | -18 | -3.86 | 22 |
| Caudate | | -16 | 28 | 16 | -4.90 | 64 |
| | | 12 | 20 | 10 | -5.55 | 151 |
| | 48 | 20 | 28 | -2 | -4.22 | 27 |
| Nucleus Accumbens | | -12 | 14 | -12 | -3.98 | 63 |
| Cerebellum Lobule VI | | -12 | -60 | -12 | -5.98 | 196 |
| Vermis | | 0 | -66 | -20 | -3.81 | 22 |

PFC = Prefrontal Cortex

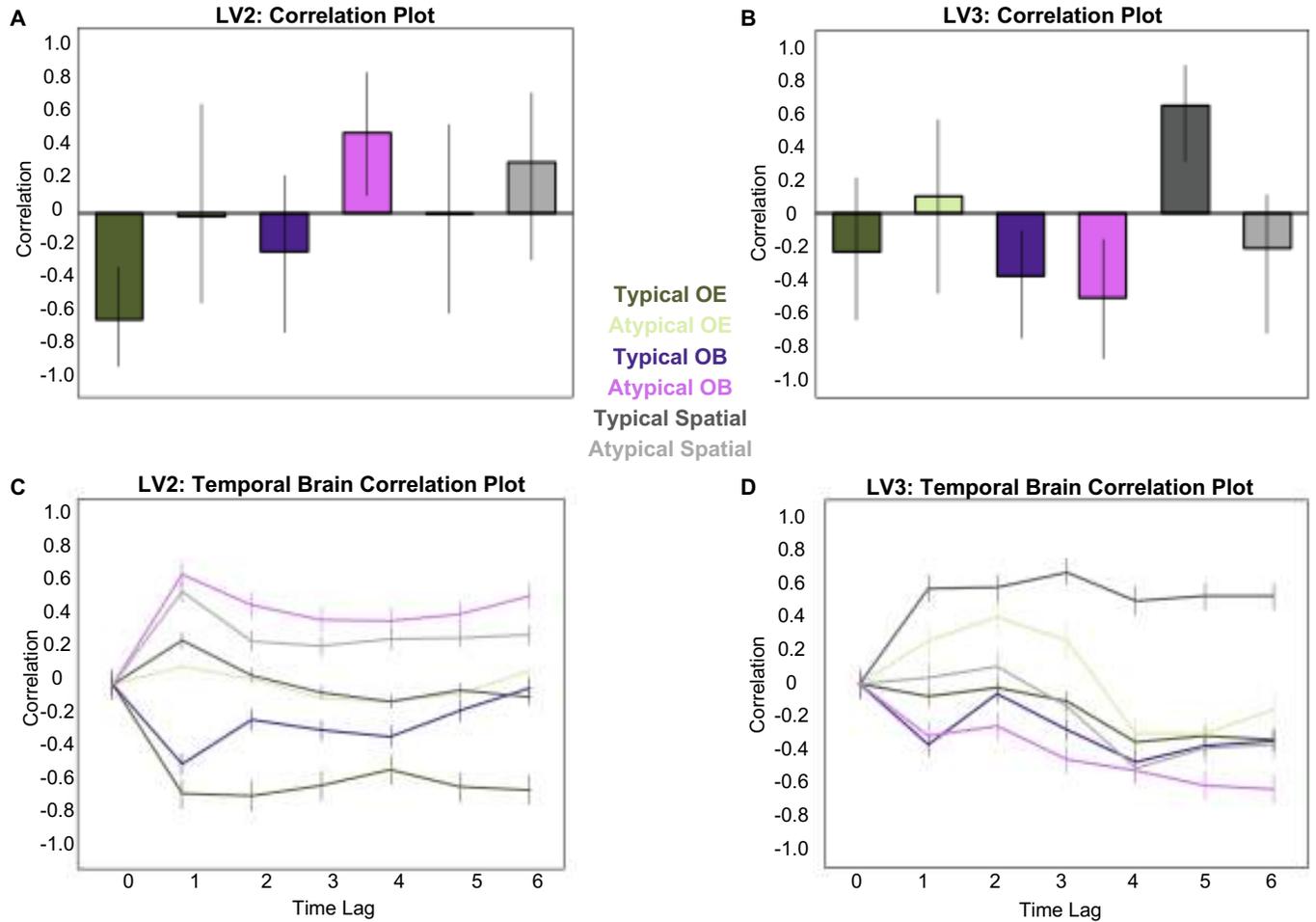


Figure 4. Hippocampal Seed PLS Results for LV2 and LV3. Correlation and temporal brain correlation plots extracted from LV2 and LV3 of the hippocampal seed PLS analysis. LV2 clearly distinguishes typical OE from atypical OB conditions throughout the retrieval period (A), which peaks during time lag one and persists across subsequent time lags (B). While LV3 assigned a significantly more negative weighting to atypical OB compared to typical OE conditions during lags four and six, the most striking differences are between OB and the typical Spatial conditions (C) which are differentiated throughout retrieval (D). Each time lag corresponds to 2.5s (i.e., one TR).

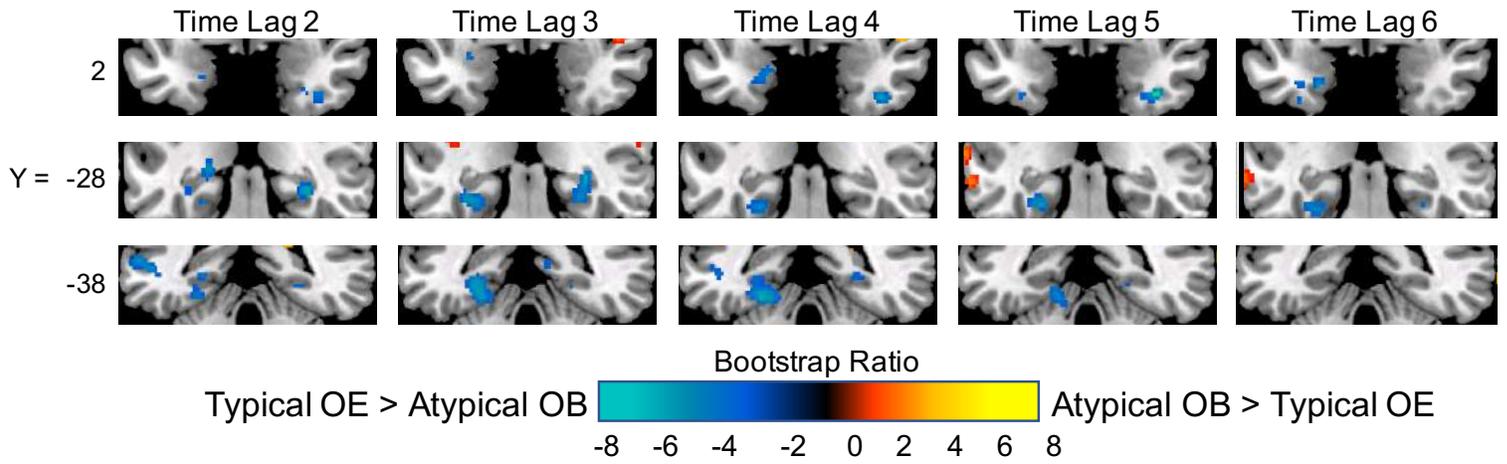


Figure 5. Within-MTL Functional Connectivity During Elaboration LV3. The pattern of functional connectivity with the left anterior hippocampus identified in LV3, which shows within-MTL differences in the OB versus typical Spatial conditions during elaboration (i.e., time lags 2 to 6). OE = Own Eyes, OB = Observer. All images depict a BSR threshold of +/- 3.

Appendix B

Table 1.

List of Statements Used in the Truth Game

| | Statement 1 | Statement 2 | Statement 3 |
|-------------------|--|---|--|
| Memory Cue | | | |
| <i>Groups</i> | A group of crows is called a murder. | A group of owls is called a parliament. | A group of bats is called a bevvv. (<i>False</i>) |
| <i>Brighton</i> | The Brighton Sea Life Centre is the world's oldest aquarium. | The University of Sussex was Established in 1961. | Brighton is the 2nd happiest place to live in the UK. (<i>False</i>) |
| <i>Berries</i> | A banana is a berry. | An avocado is a berry. | A strawberry is a berry. (<i>False</i>) |
| <i>Favorites</i> | My favorite sport is baseball. | My favorite beverage is coffee. | My favorite colour is purple. (<i>False</i>) |

Table 2.

Cued Recall Questions

| | Memory Encoding Session Question | Post-Scanning Session Question |
|------------------------------|--|---|
| Game | | |
| <i>I Spy</i> | What was your first guess? | What was your last guess? |
| <i>Categories</i> | What was the first example you came up with? | What was the last example you came up with? |
| <i>Sentence Construction</i> | What was the first word of the sentence? | What was the last word of the sentence? |
| <i>Truth Game</i> | What was the first statement? | What was the last statement? |

Appendix C

Guided Scavenger Hunt Scripts

Café. You are on a scavenger hunt and have decided to look inside this café for possible treasure. Before moving, take a minute to familiarize yourself with the environment. Enter the café, stop just inside the door, and have a look around (**1-minute mark**). Turn right and walk towards the doors straight ahead of you. Take a moment to look around. Turn around and head towards the counter. Face the counter and have a look around. Face the door and have a look around (**2-minute mark**). Turn to your right and investigate the area under the staircase. Walk along the right hand side of the café. Stop at the door and inspect the scene one more time. Turn around and return to the street.

House. You are on a scavenger hunt and have decided to look inside this house for possible treasure. Take a few seconds to look around your surroundings. Turn to your right and walk towards the coffee table. Have a look around. Walk between the sofa and the window and head towards the party table. Facing the table have a look around (**1-minute mark**). Walk towards the desk at the back of the room and look around. Head towards the bedroom area and have a look around (**2-minute mark**). Walk towards the hallway and enter the reading room to your right. Have a look around. Exit the reading room and walk towards your starting position just in front of the hallway. Turn around to face the room and have one more look.

Presence Questionnaire

To what extent did you have a sense of being in the café/house from 1 (not at all) to 7 (very much so)?

To what extent were there times during the experience when the house became the 'reality' for you, and you almost forgot about the 'real world' of the lab in which the whole experience was really taking part from 1 (never) to 7 (almost all the time)?

When you think back about your experience, do you think of the virtual house more as images you saw or more as somewhere that you visited on a scale from 1 (only as images that I saw) to 7 (somewhere that I visited)?

Guided Avatar Movements Script

1. Lift up your right arm in front of you and take it to the side
2. Lift up your left arm in front of you and take it to the side
3. Lift up your right leg
4. Lift up your left leg
5. Look down
6. Take 2 steps towards the mirror
7. Try to see yourself in the mirror
8. Crouch down and stand back up
9. Jump

10. Take 2 steps backward

Total time: 45 seconds