An embodied perspective: angular gyrus and precuneus decode selfhood in memories of naturalistic events

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Abstract

While memory encoding is often assumed to occur from an in-body (first-person) perspective, out-of-body experiences demonstrate that we can form memories from a third-person perspective. This phenomenon offers a unique opportunity to investigate how embodiment interacts with visual perspective during encoding to shape how past events are recalled. Participants formed memories for naturalistic events following a manipulation of their sense of embodiment from in-body and out-of-body perspectives and recalled them during functional scanning. Region of interest multivariate analyses examined how the angular gyrus, precuneus, and hippocampus reflected visual perspective, embodiment, and their interaction during remembering. Patterns of activity during retrieval in the left angular gyrus and bilateral precuneus predicted the combination of embodiment and visual perspective, and embodiment on its own separated from visual perspective. Decoding accuracy was not significant for any region when predicting visual perspective alone. Our results suggest that the involvement of posterior parietal regions in establishing visual perspectives within memories cannot be disentangled from embodiment. Encoding events from an embodied in-body perspective led to higher memory accuracy following repeated retrieval. These results elucidate how fundamental feelings of being located within and experiencing the world from the perspective of one's own body are integrated within memory.

Keywords: egocentric perspective, embodiment, episodic memory, fMRI, naturalistic stimuli

The ability to re-experience past events vividly and accurately through remembering is tightly linked to the awareness and perception of one's body, or bodily selfhood (e.g., (Bergouignan, Nyberg, & Ehrsson, 2014; Bréchet et al., 2020, 2019; Iriye & Ehrsson, 2022; Penaud, Yeh, Gaston-Bellegarde, & Piolino, 2023). Bodily selfhood typically involves the feeling of being located in one's body at a specific point in space (i.e., self-location), a sense of ownership over one's body (i.e., body ownership), and experiencing the world from an in-body, first-person perspective (Blanke et al., 2015). However, disturbances to the sense of bodily selfhood such as observer experiences, or out-of-body experiences, arise whereby one experiences a detachment from the physical body during an event and is afforded a view of "how the entire scene would appear … to an onlooker who sees us as well as our surroundings" (p. 469, Nigro & Neisser, 1983). Observer and out-of-body experiences are often reported in the contexts of schizophrenia and post-traumatic stress disorder (Blackmore, 2019; Reynolds & Brewin, 1999). Yet, 10-15% of the general population is estimated to have at least one observer experience over their lifetime (Blackmore, 2017, Blanke et al., 2004), leading to them to be described as "normal though unusual experiences" (p. 163, (Amorim, 2003). It remains unknown how alteration in the sense of self-location, body ownership, and visual perspective during encoding affect neural mechanisms of memory retrieval. For example, most neuroimaging studies have focused on manipulations of visual perspective during memory retrieval (Eich et al., 2009a; Freton et al., 2014a; Grol et al., 2017a; Hebscher et al., 2021; St. Jacques et al., 2017, 2018) rather than on encoding (but see Bergouignan et al., 2014). Here, we employ an innovative paradigm that allows the manipulation of visual perspective (i.e., whether an event is formed from either a natural in-body perspective or a third-person perspective) alongside feelings of self-location and body ownership (i.e., embodiment) during the formation of highly realistic

events to investigate how these fundamental aspects of selfhood are reflected in patterns of neural activity during retrieval. This research develops a new comprehension of how basic forms of selfhood rooted in the body structure higher-level aspects of selfhood tightly linked with episodic memory (Iriye & St. Jacques, 2019; Prebble et al., 2013). Clinically, insight into the relationship between visual perspective, embodiment and memory has the potential to deepen understanding of why disorders characterized by abnormal body experiences like dissociation from one's physical body, such as is the case in schizophrenia, also incur episodic memory deficits (Borda & Sass, 2015; Prebble et al., 2013; Sierra & David, 2011).

The sense of bodily selfhood is typically manipulated experimentally by capitalizing on the multisensory nature of brain mechanisms that determine own-body perception (e.g. (Guterstam, Björnsdotter, Gentile, et al., 2015a; Petkova & Ehrsson, 2008; van der Hoort et al., 2011). 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. (Guterstam & Ehrsson, 2012; O'Kane & Henrik Ehrsson, 2021). This paradigm has been used to establish ownership over an invisible body, demonstrating the incredibly plastic underpinnings of bodily selfhood (D'Angelo et al., 2017; Guterstam, Abdulkarim, et al., 2015; Kondo et al., 2018). For example, Guterstam and

colleagues (2015) and D'Angelo and colleagues (2017) asked participants wear 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 contrast, in the current study we implemented the invisible body illusion to manipulate the sense of bodily selfhood from in-body and out-of-body perspectives that included participants' own physical bodies in their field of view, mimicking clinical reports of out-of-body experiences defined by perceiving oneself from a third-person perspective (Blanke et al., 2004).

Previous research suggests that the individual components of bodily selfhood (i.e., body ownership, self-location, and visual perspective) may be supported by activity within the angular gyrus, precuneus, and hippocampus. Iriye, Chancel, & Ehrsson (2024) immersed participants in naturalistic scenes involving lifelike events while manipulating ownership over a mannequin's body aligned with participants' real bodies with synchronous and asynchronous visuotactile stimulation during functional magnetic resonance imaging (fMRI) scanning. One week later, participants retrieved these events from memory also during fMRI scanning. The authors observed that patterns of activity in regions including the left angular gyrus, right precuneus, and bilateral hippocampi predicted whether body ownership was strong (i.e., synchronous visuotactile stimulation) compared to weak (i.e., asynchronous visuotactile stimulation) during encoding. Moreover, memory reinstatement in these three regions, as measured by encoding-retrieval pattern similarity, was greater for lifelike

memories formed with strong body ownership and high levels of memory vividness, compared to weak body ownership and low memory vividness. Other research has indicated that a portion of the left angular gyrus, linked to multisensory integration and visuospatial representations of body parts (Vingerhoets, 2014), is implicated in implementing probabilistic models that dynamically and continuously generate the sense of body ownership by comparing incoming sensory information with previous perceptual experiences (Chancel et al., 2022). Actively disrupting activity in the angular gyrus through brain damage (Ionta et al., 2011) seizures (Blanke et al., 2004), or transcranial magnetic stimulation (Blanke et al., 2002) leads to out-of-body experiences involving the feeling of dissociation from one's physical body and a shift in visual perspective to an observer/out-of-body point of view. Further, lesions in the angular gyrus are associated with reduced use of in-body perspective imagery during mental navigation (Ciaramelli et al., 2010a). 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., 2018a). However, the angular gyrus may be implicated in instantiating both types of visual perspectives. 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. Thus, further research is required to elucidate the role of this region in establishing egocentric frameworks during memory retrieval. Current evidence suggests that multisensory information underpinning one's

sense of bodily selfhood is integrated with additional multimodal memory features within a common egocentric perspective in the angular gyrus.

While egocentric perspectives are established in the angular gyrus, they can be manipulated in the precuneus (St. Jacques et al., 2017, 2018). The precuneus is associated with visual mental imagery (Cavanna & Trimble, 2006; Fletcher et al., 1995) and the transformation of allocentric spatial representations stored in the hippocampus into egocentric reference frames (Byrne et al., 2007). Several studies have reported that adopting an observer perspective during memory retrieval recruits the precuneus (Faul et al., 2020; Grol et al., 2017; St. Jacques et al., 2017). 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). These conflicting findings may be explained by considering that the precuneus contributes to the construction of mental scenarios from an egocentric framework, such that adopting a more atypical observer perspective places greater demands on the involvement of this region (Iriye & St. Jacques, 2020). According to this interpretation (St. Jacques, 2019), the precuneus supports both own eyes and observer perspectives during memory retrieval. Supporting this idea, St. Jacques and colleagues (2018) reported common involvement of the precuneus when adopting a novel observer and own eyes perspective. Nonetheless, greater research is needed to clarify how different visual perspectives are represented in this region. In addition to visual perspective, the precuneus may also play a key role in bodily selfhood more widely. For example, direct cortical stimulation of the anterior precuneus leads to altered bodily sensations such as falling/dropping, floating, dizziness, and self-dissociation (Lyu et al., 2023). Together these findings suggest that the

precuneus plays a role in the ability to construct mental scenes from an embodied perspective during memory retrieval.

Beyond the parietal cortex, the hippocampus has been shown to contain information conveying an individual's sense of self-location during full-body illusions (Guterstam, Björnsdotter, Bergouignan, et al., 2015; Guterstam, Björnsdotter, Gentile, et al., 2015b), which may contribute to how memories are encoded and later retrieved. Consistent with this idea, Bergouignan and colleagues (2014) reported repetition enhancement effects in response to repeatedly retrieving memories encoded from an out-of-body perspective in the left posterior hippocampus. The strength of this hippocampal repetition enhancement effect predicted concomitant reductions in reported memory vividness (i.e., clarity of mental images during remembering) and impaired recall of episodic details for memories encoded from an out-of-body compared to in-body perspective. Conversely, repeated retrieval of realistic memories encoded from a more natural in-body perspective was linked to repetition suppression effects in the left posterior hippocampus. The authors suggested that forming memories from an out-of-body perspective disrupts encoding mechanisms in the hippocampus, which alters later activation during retrieval. However, participants in this experiment experienced only embodied in-body and out-of-body perspectives, induced by synchronous visuotactile stimulation, and thus, it is unclear whether the hippocampus would be sensitive to feelings of disembodiment during memory formation, induced by asynchronous visuotactile stimulation. In the present study we tested whether the hippocampus contained separate neural representations of embodied viewpoints using a two (embodiment: synchronous, asynchronous) x two (visual perspective: in-body, out-of-body) experimental design and a multivariate analytical approach, which is thought to reflect neural representations in a similar way to repetition suppression (Barron et al.,

2016). Together, previous findings suggest that the hippocampus may be sensitive to the combined influence of visual perspective, self-location, and body ownership when retrieving events encoded from different perspectives with the aim of supporting spatial memory processes.

We conducted the present study to investigate how visual perspective and the sense of embodiment (i.e., here body ownership and self-location) interact to shape patterns of activity within the angular gyrus, precuneus, and hippocampus during memory retrieval. Participants formed memories for a series of realistic events following an established paradigm to manipulate their sense of bodily self from in-body and out-of-body perspectives using synchronous and asynchronous visuo-tactile stimulation yielding four experimental conditions: in-body synchronous, in-body asynchronous, out-of-body synchronous, out-of-body asynchronous. Memories for these events were repeatedly recalled during functional scanning later that same day. We trained multivariate classifiers to predict whether patterns of activity within the three selected regions of interest reflected visual perspective (i.e., in-body versus out-of-body perspectives, collapsed across embodiment conditions), embodiment (i.e., synchronous versus asynchronous visuotactile stimulation, collapsed across visual perspectives), and their interaction (i.e., each of the four conditions was linked to a dissociable pattern of neural activity) during retrieval.

Regarding the angular gyrus, we hypothesized that patterns of activity would reflect the visual perspective (i.e., in-body, out-of-body), sense of embodiment (i.e. synchronous, asynchronous), and their interaction based on this region's involvement in multisensory integration of bodily signals underpinning own-body perception (i.e., Iriye et al., 2024; Chancel et al., 2023) and participation in establishing both in-body and out-of-body egocentric perspectives (Bonnici et al., 2018; Grol et al., 2017; St. Jacques et al., 2017).

Concerning the precuneus, we expected that patterns of activity during memory retrieval would reflect the sense of embodiment present during encoding of the event, due to recent research linking stimulation of this region to altered states of bodily awareness (Lyu et al., 2023). We also predicted that the activity in the precuneus would not represent visual perspective on its own separated from embodiment, as previous research has shown that the precuneus supports retrieval from both in-body and out-of-body perspectives (e.g., St. Jacques et al., 2018). Instead, we expected that the patterns of activity in the precuneus would reflect the interaction between visual perspective and embodiment as direct stimulation of this region leads to dissociative bodily states (Lyu et al., 2023), which are more commonly linked to out-of-body compared to in-body perspectives (Blanke et al., 2004). For the hippocampus, we predicted that patterns of activity in this region would reflect visual perspective, embodiment, and their interaction due to reports of its involvement in memory studies manipulating embodiment (Iriye et al., 2024), and visual perspective and embodiment together (Bergouignan et al., 2014).

Materials and Methods

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. Functional scanning data from four participants was excluded due to a technical issue. Thus, the final analysis was performed on 24 participants (14 women, 10 men; *mean age* = 20.46, *SD* = 2.21; *mean years of education* = 14.96, *SD* = 1.68). The sample size in the

present study (*N* = 24) is comparable with the sample size of previous neuroimaging studies investigating the role of bodily selfhood on memory (e.g., Bergouignan et al., 2014: *N* = 21; Iriye et al., 2024: *N* = 24).

Procedure

Overview. The experiment involved five main phases: illusion induction, event encoding, immediate memory test, retrieval during fMRI scanning, and a post-scanning memory test. The first part of the experiment involved altering participants' sense of bodily ownership, self-location, and embodiment with two well-established illusion inductions known as the full-body illusion (Petkova & Ehrsson, 2008) and invisible body illusion (Guterstam, Abdulkarim, et al., 2015). During the illusion induction, participants viewed themselves from either an in-body or out-of-body visual perspective while receiving synchronous (i.e., sync) or asynchronous (i.e., 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, the event encoding task involved asking participants to engage in a series of brief, realistic events consisting of four separate word games played with the experimenter. Then, during an immediate memory test, participants practiced vividly retrieving each game with their closed eyes immediately after each game was complete. They also 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 own eyes perspective taking, observer perspective taking, vividness, emotional intensity, and perceived memory accuracy on seven-point Likert scales. This process was repeated for the remaining three conditions. Later that day, participants retrieved memories for the events during fMRI scanning. They were asked to repeatedly retrieved memories for each of the events, in addition to rating visual perspective (on

separate in-body and out-of-body scales) and vividness. Finally in a post-scanning memory test, they were asked additional novel questions about each event and provided ratings of emotional intensity and perceived memory accuracy. Below we discuss each of the experimental phases in detail.

Illusion Inductions. Two videos, one from an out-of-body perspective and one from an in-body perspective were recorded to be used in the illusion induction. For the out-of-body perspective video, 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 and placed behind the participant. 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 presenting a view of the participant's back body, as if they were standing behind themself. After video recording started, 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, et al., 2015). 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, et al., 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 a small, flexible tripod attached to the front of the HMD unit to create a video from an in-body perspective (see Figure 1B). Then, 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 (Free Version; Fleischman, 2000), which allowed them to be visible both inside the HMD unit and on the desktop computer screen. Each video was 62.5 seconds in length.

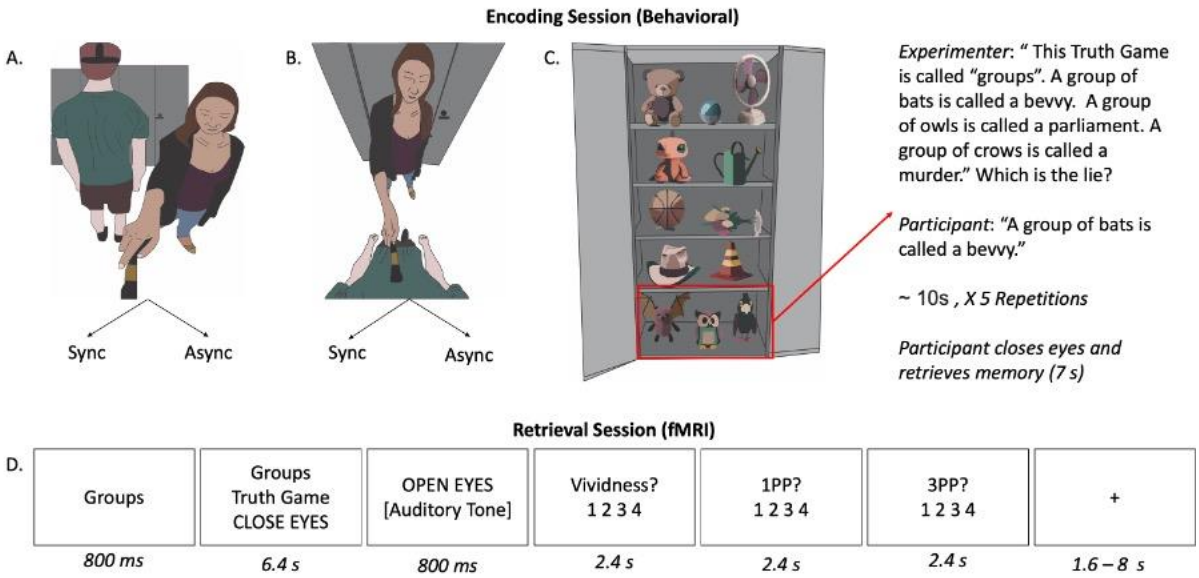

Figure 1. Participants wore a virtual HMD and viewed a live feed of the experimental room from either an in-body (A) or out-of-body perspective (B). In half of the trials, participants received synchronous (sync) visuotactile stimulation to induce a sense of ownership either over their own body in the own eyes condition, or an invisible body located under the camera in the observer condition. In the other half of the trials, the experimenter administered asynchronous (async) visuotactile stimulation to reduce the sense of ownership over the participant's real body (own eyes condition) or the invisible body located below the camera (observer condition). The participants then played a series of word games with the experimenter based on unique items located in the cabinet in front of them (C). There were four games in each round (Truth Game, I Spy, Categories, Sentence Construction) and each game was repeated a total of five times. At the end of the last repetition of each game, participants closed their eyes and retrieved a memory for the game for 7 s before moving on to the next game. At the end of each round of four games, participants completed a cued recall accuracy test for each word game and subjective ratings of vividness, emotional intensity, and the degree to which they retrieved their memory from a 1PP and 3PP on separate scales. Later that day, participants retrieved memories for the word games during functional scanning, and rated the vividness of their mental imagery and the perspective adopted during retrieval on separate own eyes and observer scales (D). Participants completed a second cued recall test and rated the emotional intensity and belief in memory accuracy associated with their memories post-scanning.

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 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. The experimenter applied brushstrokes to the participant's body either synchronously or asynchronously with the timing of brushstrokes in the video in the same location as seen in the video. Seen and felt touches in the asynchronous condition were temporally spaced such that there was no overlap. 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 captured with the Ricoh Theta camera using a custom application implemented in Unity 5.3.0. The transition from recorded video to live stream was less than five seconds.

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 (see Figure 1C). 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). 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 Supplemental Table 1). 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 bevvy", 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 1C). The participant next guessed which statement was the lie (i.e., "a group of bats is called a bevvy").

The experimenter announced the game type (i.e., "I Spy", "categories", "sentence construction2, and "truth game") and a unique title (e.g. groups) at the start of each game. 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.

Table 1. Word Game Stimuli

Game	Memory Cue	Stimuli
I Spy	Blue	Watering Can, Ball
	White	Fan, Plunger
	Orange	Basketball, Cone, Toy Dinosaur
	Brown	Cardboard box, Hat
Categories	Animals	Toy Dog, Toy Parrot
	Vegetables	Butternut Squash, Carrot
	Sports	Kettlebell, Bowling Pin
	Music	Ukulele, Headphones
Sentence Construction	Plant	Potted Plant
	Wine	Wine Bottle
	Basket	Easter Basket
	Clock	Wall Clock
Truth Game	Groups	Toy Bat, Toy Owl, Toy Crow
	Brighton	University of Sussex Sweatshirt, Photo of a Happy Face Emoji, Toy Ocotpus
	Berries	Two Avocados, 5 Bananas, 1 Bowl of Strawberries
	Favorites	Baseball Cap, Purple Gloves, Coffee Bodum

Immediate Memory Test. After each round of four games, participants were instructed to remove the HMD unit and answered a series of questions. The first was a questionnaire designed to assess bodily sensations experienced during the illusion induction and while playing the games, adapted from Guterstam and colleagues (2015a). It included three statements designed to assess the strength of the embodiment illusion (see Table 2, I1 to I3) and three control statements to assess a participant's susceptibility to demand characteristics (see Table 2, C1 to C3) 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), with 0 reflecting neutral. Next, participants answered one cued recall question from each game (see Supplemental Table 2), and rated their memory for each game on 7-point subjective ratings according to vividness (1 = a little, 7 = a lot), emotional intensity (1 = a little, 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 1PP and 3PP perspectives (1 = a little, 7 = exclusively 1PP/3PP). Participants were instructed that 1PPs referred to visualizing their mental scene from the perspective of their own eyes such that they did not see themselves in the event, whereas 3PPs referred to being able to see themselves in the mental scene as if from the perspective of an observer.

Once participants had answered all questions, the next embodiment illusion was induced. This process was repeated for each of four conditions: in-body sync, in-body async, out-of-body sync, out-of-body async. Thus, participants played four games in each condition. The order of conditions, games, and stimuli within each game were allocated randomly for each participant.

Table 2. Bodily Illusion Questionnaire Items

Statement Number	Visual Perspective	Statement
I1	Out-of-Body	I felt the touch of the brush in empty space in the location where I saw the brush moving
I2	Out-of-Body	I experienced that the touch I felt was caused by the brush moving in the empty space.
I3	Out-of-Body	It felt as if I had an invisible body.
C1	Out-of-Body	I could no longer feel my body.
C2	Out-of-Body	I felt as if I had two bodies.
C3	Out-of-Body	When I saw the brush moving, I experienced the touch on my back.
I1	In-Body	I felt the touch of the brush on the body I saw in the location where I saw the brush moving.
I2	In-Body	I experienced that the touch I felt was caused by the brush touching the body I saw.
I3	In-Body	It felt as if the body I saw was my body.
C1	In-Body	I could no longer feel my body.
C2	In-Body	I felt as if I had two bodies.
C3	In-Body	When I saw the brush moving, I experienced the touch on my back.

I = Illusion Statement; C = Control Statement

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 memory 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., groups) and game title (e.g., truth game). 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 1PP perspective, the degree to which they retrieved the event from an 3PP perspective, and the degree of vividness associated with memory retrieval, each on four-point scales from one = low to four = high. The order of the 1PP and 3PP 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. An example trial is depicted in Figure 1D.

There were 12 functional runs consisting of 16 trials (i.e., one trial per event, four 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.

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.

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. Functional images were realigned within and across runs to correct for head movement, segmented into gray matter, white matter, and cerebrospinal fluid, co-registered to the participant's anatomical image, and spatially normalized to the Montreal Neurological Institute (MNI) template. BOLD signal response patterns for each trial were estimated using a general linear model (GLM). A regressor was estimated for each trial in the twelve functional runs, resulting in 16 beta estimates per run (i.e., 48 trials per condition). 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. The functional data was denoised using the RobustWLS Toolbox (Diedrichsen & Shadmehr, 2005).

Behavioral Analyses

The illusion induction questionnaire data was assessed by submitting average illusion minus control statement scores for each condition (e.g., Iriye et al., 2022; 2024) to a 2 (visual perspective: in-body, out-of-body) x 2 (embodiment: sync, async) repeated-measures ANOVA. Illusion minus control statement scores reflect the strength of the illusion induction, taking into account participants' susceptibility to answer positively to the control statements. 1PP ratings, 3PP ratings, vividness ratings, emotional intensity ratings, and belief in memory accuracy ratings from the immediate memory test, scanning, and post-scanning memory test were assessed with eight separate 2 (visual perspective: in-body, out-of-body) x 2 (embodiment: sync, async) repeated-measures ANOVAs. We controlled for multiple comparisons using Bonferroni corrections. Outliers were defined as data points that were 1.5 interquartile ranges below the first quartile or above the third quartile. All analyses were conducted with and without outliers to determine their influence on the results and are reported below.

Multivariate Decoding

ROI Analyses: Classifier Accuracy Across Conditions. We created individual masks of the left and right hemispheres of angular gyrus, precuneus, and hippocampus in WFU Pickatlas (Maldjian et al., 2003) based on 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 et al., 2002) and resampled to 2mm cubic voxels to match the dimension of the beta estimates obtained from the GLM analysis (see Figure 2).

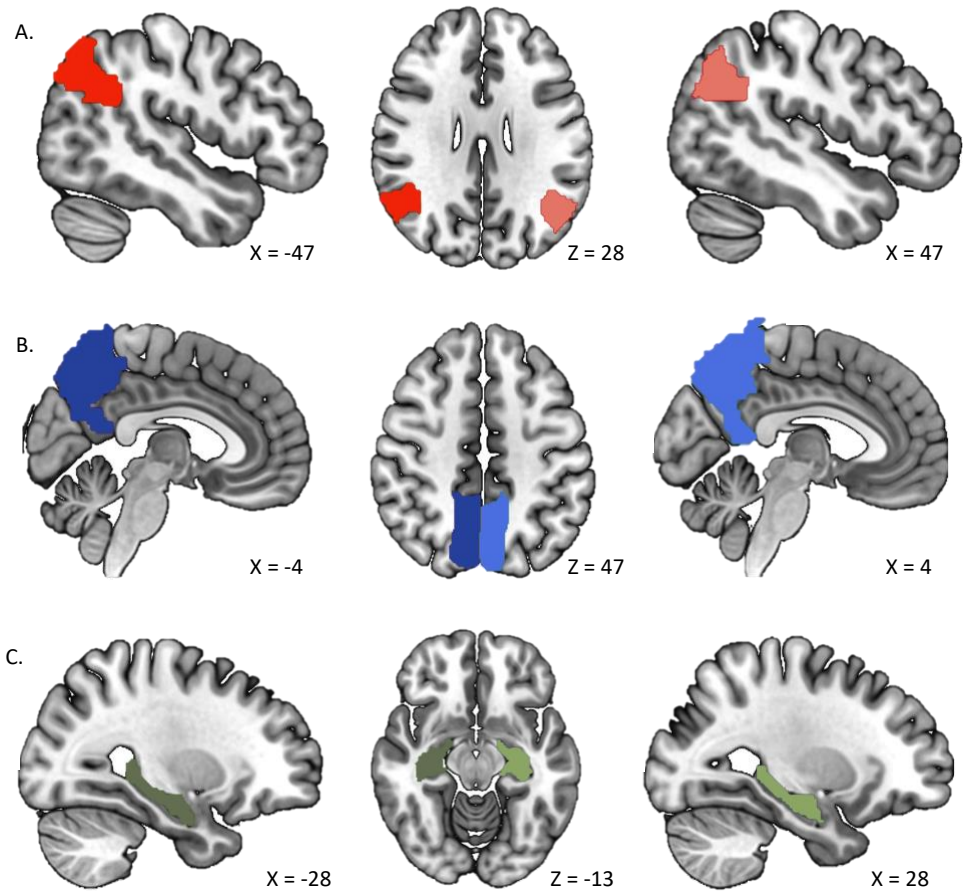

Figure 2. ROIs for the left and right angular gyrus (A), precuneus (B), and hippocampus (C) as ROIs. Separate masks were created for the left and right hemispheres of each region.

We conducted three separate analyses for each of the six ROIs to test whether patterns of activity during memory retrieval in each of the ROIs predicted 1) visual perspective (i.e., in-body or out-of-body) initially experienced during encoding, 2) embodiment (i.e., sync or async visuotactile stimulation) initially experienced during encoding, and 3) the interaction between visual perspective and embodiment (i.e., the condition of each trial: in-body sync, in-body async, out-of-body sync, out-of-body async). We calculated the decoding accuracy (i.e., number of correctly classified trials / number of

total trials) for each participant within each ROI using a linear discriminant analysis (LDA) classifier. The data was divided into training and test sets using k-fold cross-validation. Subject-level accuracies were submitted to a two-sided, one-sample t-test against a null hypothesis of chance-level classification accuracy (i.e., 50% for the visual perspective and embodiment analyses, 25% for the combination analysis). We corrected for multiple comparisons by applying Bonferroni-Holm corrections. All multivariate analyses were implemented in the CoSMoMVPA toolbox (Oosterhof et al., 2016).

For the embodiment analysis only, we correlated participants' decoding accuracy minus chance scores in ROIs showing significantly above chance decoding accuracy with their reported strength of the illusion induction. Illusion induction strength was calculated by subtracting average control statement scores from average illusion statement scores from the Bodily Illusion Questionnaire, collapsed across the in-body and out-of-body conditions. We performed this analysis both on the whole group of participants (N = 24) and on the subset who were classified as responders to the illusion (N = 17). A participant was classified as a responder if their average illusion (i.e., mean rating from statements I1-I3, Table 2) minus control rating score (i.e., mean rating from statements C1-C3, Table 2) in the sync condition was greater than or equal to one, averaged over ratings given for in-body and out-of-body perspectives. This analysis revealed whether classifier performance scaled with participants' sense of embodiment during event encoding. A Pearson correlation coefficient was calculated to estimate the strength of each correlation as the data was normally distributed. Outliers were defined as data points that were 1.5 interquartile ranges below the first quartile or above the third quartile. All analyses were conducted with and without outliers to determine their influence on the results and are reported below.

ROI Analyses: Classifier Accuracy Per Condition. We calculated decoding accuracy scores per each class (i.e., visual perspective analysis: in-body, out-of-body; embodiment analysis: sync, async: interaction analysis: in-body sync, in-body async, out-of-body sync, out-of-body async), as opposed to generally across classes, for the ROIs which exhibited significantly above chance decoding accuracy averaged across conditions in the previous analyses predicting visual perspective, embodiment, or their interaction based on patterns of activity during retrieval. These analyses determined whether classifier performance was driven by a particular class relative to the other(s), which would imply that the ROI contained more information relevant to that class. Alternatively, equal classifier performance across classes would suggest that the ROI was not biased by a particular class. For analyses with two classes (e.g., embodiment; sync, async), we performed a one-sample t-test, and for the analyses with four classes (e.g., in-body sync, in-body async, out-of-body sync, out-of-body async) we performed a 2 (visual perspective: in-body, out-of-body) x 2 (embodiment: sync, async) repeated measures ANOVA.

Whole-brain searchlight analyses. We conducted three wholebrain searchlight analyses to determine whether patterns of activity during memory retrieval in any additional areas outside of the pre-specified ROIs could predict 1) visual perspective, 2) embodiment, or 3) their interaction. For each subject, a sphere comprised of 100 voxels was fitted around each voxel in the acquired volumes to create searchlight maps for each participant that reflected the classification accuracies determined by k-fold cross-validation estimated by a LDA classifier. Chance-level accuracy (i.e., 50% for the visual perspective and embodiment analyses, and 25% for the combination analysis) was subtracted from each voxel in each participant's classification accuracy map. We investigated group-level effects by submitting the resulting subject-specific classification accuracy maps to a one-sample t-

test against a null hypothesis of chance-level accuracy (i.e., 0). The resulting group-level classification accuracy map was thresholded at $p_{FWE} < .05$ to correct for multiple comparisons.

Results

Behavioral Results

Event encoding: Illusion Induction Questionnaire. A 2 (Embodiment: sync, async) x 2 (Visual Perspective: in-body, out-of-body) repeated measures ANOVA on average illusion minus control statement ratings found main effects of both embodiment, $F(1, 23) = 24.35$, $p < .001$, $\eta_p2 = .51$, and visual perspective, $F(1, 23) = 21.66$, $p < .001$, $\eta_p2 = .49$. There was also an interaction between embodiment and visual perspective, $F(1, 23) = 5.40$, $p = .029$, $\eta_p2 = .19$. Follow-up pairwise t-tests confirmed that illusion minus control statement ratings were higher in the synchronous compared to asynchronous conditions for both in-body, t (23) = 4.69, $p = .004$, Cohen's d = 1.34, and out-of-body perspectives, t (23) = 3.35, $p = .008$, Cohen's d = .69 (see Figure 3)[1]. For means and standard deviations for each condition, see Table 3. See Supplemental Figure 1 for the results of individual questionnaire items.

[1] Removing three outliers from the data led to a similar pattern of results. There was a main effect of embodiment, $F(1, 20) = 29.29$, $p < .001$, $\eta_p2 = .59$, and visual perspective, $F(1, 20) = 29.60$, $p < .001$, $\eta_p2 = .60$. The interaction was not significant, $F(1, 20) = 3.16$, $p = 09$, $\eta_p2 = .14$. Synchronous compared to asynchronous visuotactile stimulation to greater illusion minus control ratings, collapsed across visual perspectives, t (20) = 5.41, $p < .001$, Cohen's d = 1.22, demonstrating that the illusion worked as expected in both in-body and out-of-body conditions. In-body compared to out-of-body perspectives led to higher illusion minus control ratings, t (20) = 5.44, $p < .001$, Cohen's d = .84.

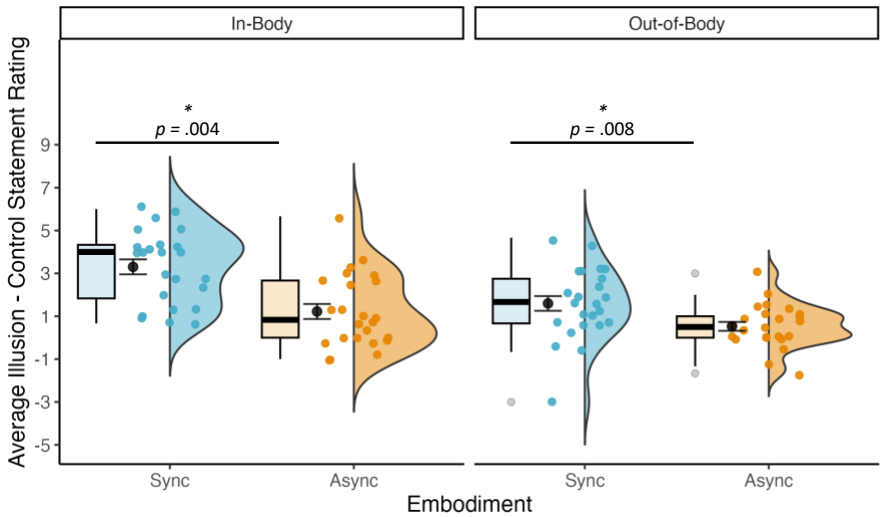

Figure 3. Average illusion minus control statement ratings were higher in the synchronous compared to asynchronous conditions for both in-body and out-of-body perspectives, indicating that the illusion worked as expected. Sync = synchronous, Async = asynchronous. ⊥ = mean +/- standard error.

Table 3. Illusion Induction Questionnaire Results

Statement Type	Visual Perspective	Embodiment	Mean (Standard Deviation)
Illusion	In-Body	Sync	1.31 (1.95)
		Async	-0.42 (2.17)
	Out-of-Body	Sync	0.65 (1.89)
		Async	-0.24 (1.97)
Control	In-Body	Sync	-0.67 (2.78)
		Async	-0.92 (2.06)
	Out-of-Body	Sync	-.31 (2.19)
		Async	-0.44 (1.90)

* Sync = synchronous, Async = asynchronous

Immediate memory test. A 2 x 2 repeated measures ANOVA with visual perspective (in-body, out-of-body) and embodiment (sync, async) conducted on average cued recall accuracy scores did not reveal a main effect of visual perspective, $F(1,23) = .49$, $p = .49$, $\eta_p2 = .02$, embodiment, $F(1,23) < .001$, $p = 1.00$, $\eta_p2 < .001$, or an interaction, $F(1,23) = 2.09$, $p = .16$, $\eta_p2 = .08$[2]. Thus, these findings suggest that there were no differences in immediate memory recall between conditions. To assess potential differences in visual perspectives at immediate retrieval between conditions, we conducted a 2 (visual perspective: in-body, out-of-body) x 2 (embodiment: sync, async) repeated measures ANOVA for 1PP and 3PP ratings separately. The analysis of 1PP ratings revealed an expected main effect of visual perspective, $F(1,23) = 57.98$, $p < .001$, $\eta_p2 = .72$, where 1PP ratings were higher in the in-body ($M = 5.86$, $SD = 1.35$) compared to out-of-body ($M = 3.77$, $SD = 1.66$) perspective (see Figure 4A). There was no significant main effect of embodiment, $F(1,23) = 2.53$, $p < .13$, $\eta_p2 = .10$ or visual perspective x embodiment interaction, $F(1,23) = 0.16$, $p = .70$, $\eta_p2 = .01$[3]. For the 3PP ratings, there was a significant main effect of visual perspective, $F(1,23) = 70.49$, $p < .001$, , $\eta_p2 = .75$, indicating higher 3PP ratings in out-of-body ($M = 4.01$, $SD = 1.85$) compared to in-body ($M = 1.74$, $SD = 1.20$) perspectives (see Figure 4B). There was no main effect of embodiment, $F(1,23) = .52$, $p = .48$, $\eta_p2 = .02$. The interaction between visual perspective and embodiment was significant, $F(1,23) = 5.53$, $p = .03$, $\eta_p2 = .19$, but did not reveal any differences between synchronous and asynchronous visuotactile stimulation in

[2] Removing the eight outliers from the data led to the same pattern of results. There was no main effect of visual perspective, $F(1,15) = 2.14$, $p = .16$, $\eta_p2 = .13$, embodiment, $F(1,15) < .001$, $p = 1.00$, $\eta_p2 < 0.001$, or an interaction, $F(1,15) < .001$, $p = 1.00$, $\eta_p2 < .001$.

[3] Removing the three outliers from the data led to the same pattern of results. There was a significant main effect of visual perspective, $F(1,20) = 72.03$, $p < .001$, $\eta_p2 = .78$, where 1PP ratings were higher in the in-body ($M = 6.13$, $SD = 1.07$) compared to out-of-body condition ($M = 3.80$, $SD = 1.65$). There was no main effect of embodiment, $F(1,20) = 1.72$, $p = .21$, $\eta_p2 = .08$, or interaction, $F(1,20) = .01$, $p = .91$, $\eta_p2 < .001$.

either the in-body (sync: *M* = 1.62, *SD* = 1.10 ; async: *M* = 1.87, *SD* = 1.09) or out-of-body (sync: *M* = 4.27, *SD* = 1.52 ; async: *M* = 3.75, *SD* = 1.80) perspective, *p*'s > .09[4].

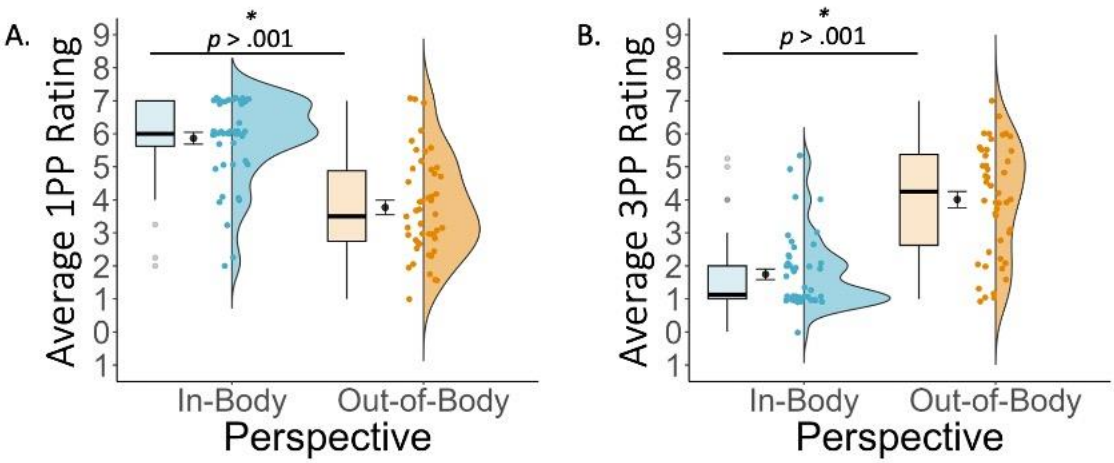

Figure 4. As expected, average OE ratings were higher in the in-body perspective (A), whereas average OB ratings were higher in the out-of-body perspective (B). ⊥ = mean +/- standard error.

For the vividness ratings, a 2 (visual perspective: in-body, out-of-body) x 2 (embodiment: sync, async) did not find a main effect of visual perspective, $F(1,23) = .25$, $p = .62$, , $\eta_p2 = .01$, embodiment, $F(1,23) = .34$, $p = .56$, , $\eta_p2 = .02$, or interaction, $F(1,23) = .05$, $p = .83$, , $\eta_p2 = .002$[5]. Similarly, there was was no main effect of visual perspective, $F(1,23) = 2.39$, $p = .14$, , $\eta_p2 = .10$, embodiment, $F(1,23) = .04$, $p = .84$, , $\eta_p2 = .002$, or interaction, $F(1,23) = 1.96$, $p = .18$, , $\eta_p2 = .08$ for the emotional intensity ratings. The same was the case for the belief in memory accuracy ratings (visual perspective: $F(1,23) = 2.28$, $p = .14$, $\eta_p2 = .09$; embodiment: $F(1,23) = 2.06$, $p = .16$, $\eta_p2 = .08$; interaction: $F(1,23) = .33$, $p = .57$, $\eta_p2 = .01$).

[4] Removing the two outliers from the data led to the same pattern of results. There was a significant main effect of visual perspective, $F(1,21) = 74.51$, $p < .001$, $\eta_p2 = .78$, where 3PP ratings were higher in the out-of-body (*M* = 3.88, *SD* = 1.86) compared to in-body condition (*M* = 1.49, *SD* = 0.84). There was no main effect of embodiment, $F(1,21) = 0.26$, $p = .62$, $\eta_p2 = .01$, or interaction, $F(1,21) = 4.14$, $p = .06$, $\eta_p2 = .17$.

[5] Removing the one outlier in the data led to the same pattern of results. There was no main effect of visual perspective, $F(1,22) = .80$, $p = .38$, $\eta_p2 = .04$, or visuotactile stimulation, $F(1,22) = 1.83$, $p = .19$, $\eta_p2 = .08$, and no interaction, $F(1,22) = .30$, $p = .590$, $\eta_p2 = .01$.

Together, the results indicate that the visual perspective manipulation was successful such that participants could recall whether events were experienced from an in-body or out-of-body perspective immediately following memory encoding. Importantly, there were no significant differences between the conditions for memory phenomenology, such that vividness, emotional intensity, and perceived memory accuracy were equal across the conditions.

In-scanner subjective ratings. The analysis of in-scanner visual perspective ratings revealed the same pattern of effects observed in the immediate memory test (see Figure 5). For the 1PP ratings, there was a significant effect of visual perspective, $F(1,23) = 26.25$, $p < .001$, $\eta_p2 = .53$, indicating higher 1PP ratings in the in-body ($M = 3.05$, $SD = .97$) compared to out-of-body perspective conditions ($M = 2.49$, $SD = 1.07$). There was no main effect of embodiment, $F(1,23) = 1.02$, $p = .32$, $\eta_p2 = .04$, or interaction effect, $F(1,23) < .001$, $p = .97$, $\eta_p2 < .001$[6]. For the 3PP ratings, there was also a significant effect of visual perspective, $F(1,23) = 25.21$, $p < .001$, $\eta_p2 = .52$. 3PP ratings were higher for the out-of-body perspective conditions ($M = 2.22$, $SD = 1.11$) compared to the in-body conditions ($M = 1.65$, $SD = .88$). There was no main effect of embodiment, $F(1,23) = .68$, $p = .42$, $\eta_p2 = .03$, or interaction effect, $F(1,23) = .006$, $p = .94$, $\eta_p2 < 0.001$[7]. Turning to the vividness ratings, there was no main effect of visual perspective, $F(1,23) = .65$, $p = .43$, $\eta_p2 = .03$, or embodiment, $F(1,23) =$

[6] Removing the one outlier from the data led to the same pattern of results. There was a main effect of visual perspective, $F(1,22) = 27.93$, $p < .001$, $\eta_p2 = .56$, indicating higher ratings in the in-body ($M = 3.12$, $SD = 0.91$) compared to out-of-body condition ($M = 2.53$, $SD = 1.06$). There was no main effect of embodiment, $F(1,22) = .31$, $p = .31$, $\eta_p2 =.04$, or interaction, $F(1,22) < .001$, $p =.99$, $\eta_p2 <.001$.

[7] Removing the two outliers from the data led to the same pattern of results. There was a main effect of visual perspective, $F(1,21) = 5.18$, $p < .001$, $\eta_p2 =.52$, indicating higher ratings in the in-body ($M = 2.13$, $SD = 1.08$) compared to out-of-body condition ($M = 1.63$, $SD = .87$). There was no main effect of embodiment, $F(1,21) = .55$, $p = .47$, $\eta_p2 =.03$, or interaction, $F(1,21) = .40$, $p =.54$, $\eta_p2 =.02$.

2.48, p = .13, η_p2 = .10, or an interaction, $F(1,23)$ = 61, p = .44, η_p2 = .03[8]. 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.

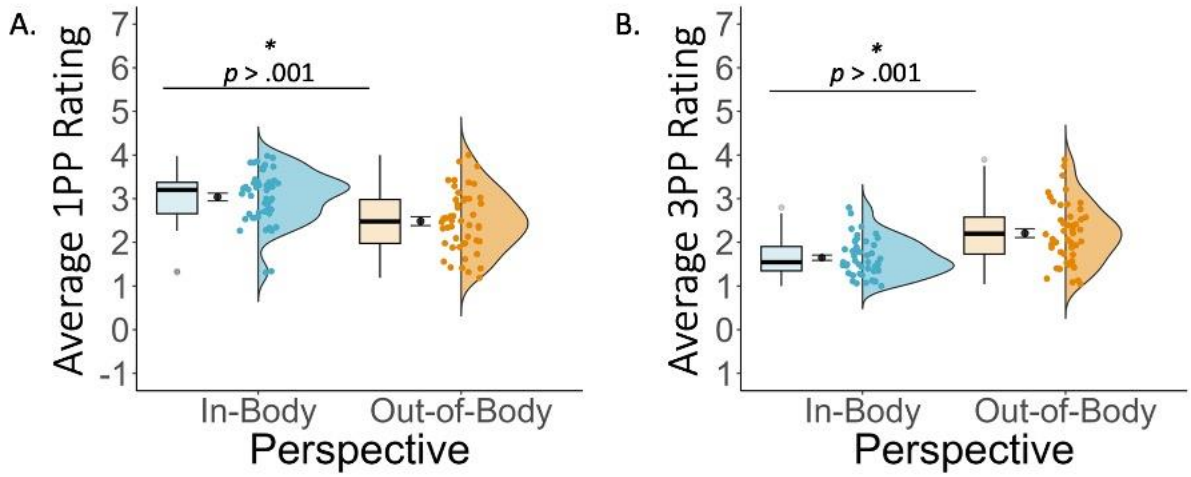

Figure 5. Average in-scanner 1PP ratings were higher in the in-body perspective (A), whereas average in-scanner 3PP ratings were higher in the out-of-body perspective (B). ⊥ = mean +/- standard error.

Post-scanning cued recall and subjective ratings. The analysis of cued recall accuracy revealed a marginally significant effect of visual perspective, $F(1,23)$ = 4.39, p = .05, η_p2 = .16, which was qualified by an interaction between visual perspective and embodiment n, $F(1,23)$ = 5.37, p = .03, η_p2 = .19. Follow-up post-hoc test revealed that memory accuracy was higher in the in-body sync condition compared to the out-of-body sync condition, p = .02 (Table 3)[9]. Turning to the emotional intensity ratings, there was no main effect of visual perspective, $F(1,23)$ = .74, p = .40, η_p2 = .03, embodiment, $F(1,23)$ = .05, p = .83, η_p2 = .002, or interaction, $F(1,23)$ = .05, p = .83, η_p2 = .002. Similarly for the belief in

[8] Removing the one outlier from the data led to the same pattern of results. There was no main effect of visual perspective, $F(1,22)$ = 3.90, p = .06, η_p2 = .15, embodiment, $F(1,22)$ = .71, p = .41, η_p2 = .03, or interaction, $F(1,22)$ = .24, p = .63, η_p2 = .01.

[9] Removing the three outliers from the data led to the same pattern of results. There was a marginally significant effect of visual perspective, $F(1,20)$ = 4.03, p = .06, η_p2 = .17, which was qualified by a significant interaction between visual perspective and embodiment, $F(1,20)$ = 5.39, p = .03, η_p2 = .21. The in-body sync condition (M = .99, SD = .06) was associated with higher cued recall accuracy compared to the out-of-body sync condition (M = .89, SD = .15), p = .046.

memory accuracy ratings, there was no main effect of visual perspective, $F(1,23) = 1.97$, $p = .17$, $\eta_p2 = .08$, embodiment, $F(1,23) = .57$, $p = .46$, $\eta_p2 = .22$, or interaction, $F(1,23) = 1.61$, $p = .22$, $\eta_p2 = .07$[10].

Table 3. Session 2: Mean cued recall accuracy scores (standard deviation)

	Synchronous	**Asynchronous**
In-body	.97 (.08)	.89 (.13)
Out-of-Body	.87 (.18)	.89 (.15)

Thus, average illusion statement scores were higher following sync compared to async visuotactile stimulation for events encoded from an in-body perspective and out-of-body perspective. Post-scanning cued recall accuracy was higher in the in-body perspective compared to out-of-body perspective only in the synchronous condition. 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.

Multivariate Decoding Analyses Results: ROI Analyses

Visual perspective. Patterns of activity during retrieval did not predict the visual perspective (i.e., in-body, out-of-body) of a given trial significantly greater than chance in any of the ROIs after applying Bonferroni-Holm corrections to account for multiple comparisons (see Figure 6)[11].

[10] Removing the one outlier from the analysis led to the same pattern of results. There were no main effects of visual perspective, $F(1,22) = 1.02$, $p = .32$, $\eta_p2 = .04$, embodiment, $F(1,22) = .31$ $p = .59$, $\eta_p2 = .01$, or interaction, $F(1,22) = .69$, $p = .41$, $\eta_p2 = .03$.

[11] Removing the two outliers of the data from the right precuneus did not affect the results, $p = .026$.

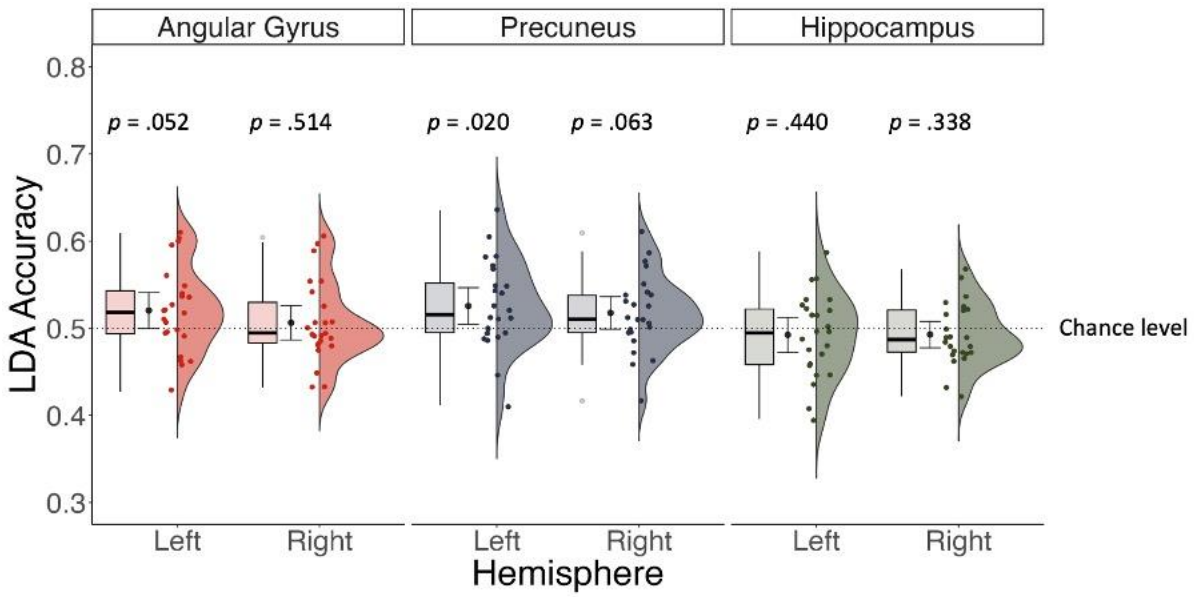

Figure 6. Decoding accuracy was no different from chance in any of the ROIs when predicting visual perspective based on patterns of activity during memory retrieval after correcting for multiple comparisons. ⊥ = mean decoding accuracy +/- 95% confidence interval.

Embodiment. Patterns of voxel activation during retrieval in both the left angular gyrus, $t(23) = 3.965$, $p = .006$, Cohen's d = 0.791 ($M = .529$, $SD = .035$), left precuneus, $t(23) = 3.83$, $p = .009$, Cohen's d = .787 ($M = .537$, $SD = .047$), and right precuneus, $t(23) = 3.277$, $p = .003$, Cohen's d = .674 ($M = .531$, $SD = .046$), distinguished the embodiment associated with memory encoding (see Figure 7).

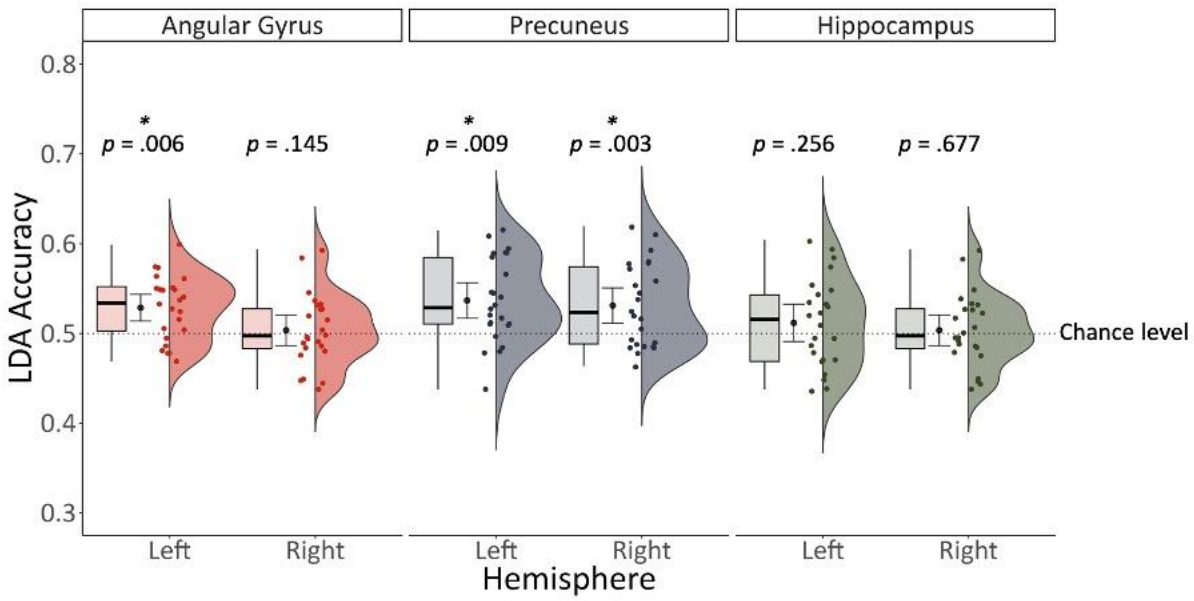

Figure 7. Decoding accuracy predicting embodiment was significantly greater than chance in the left angular gyrus, left precuneus, and right precuneus. ⊥ = mean decoding accuracy +/- 95% confidence interval.

Visual Perspective x Embodiment Interaction. The LDA classifier was able to predict the condition (i.e., in-body sync, in-body async, out-of-body sync, out-of-body async) associated with a given trial based on patterns of activity during retrieval in the left angular gyrus, $t(23) = 4.674$, $p = .001$, Cohen's d = .954 ($M = .291$, $SD = .043$; see Figure 8). The same was also true for both the left precuneus, $t(23) = 4.488$, $p = .001$, Cohen's d = .905 ($M = .288$, $SD = .042$), and right precuneus $t(23) = 3.191$, $p = .001$, Cohen's d = .659 ($M = .277$, $SD = .041$)[12].

[12] Removing the outlier from the left precuneus data led to the same results, $t(22) = 4.36$, $p = .002$, Cohen's d = .919 ($M = .284$, $SD = .037$).

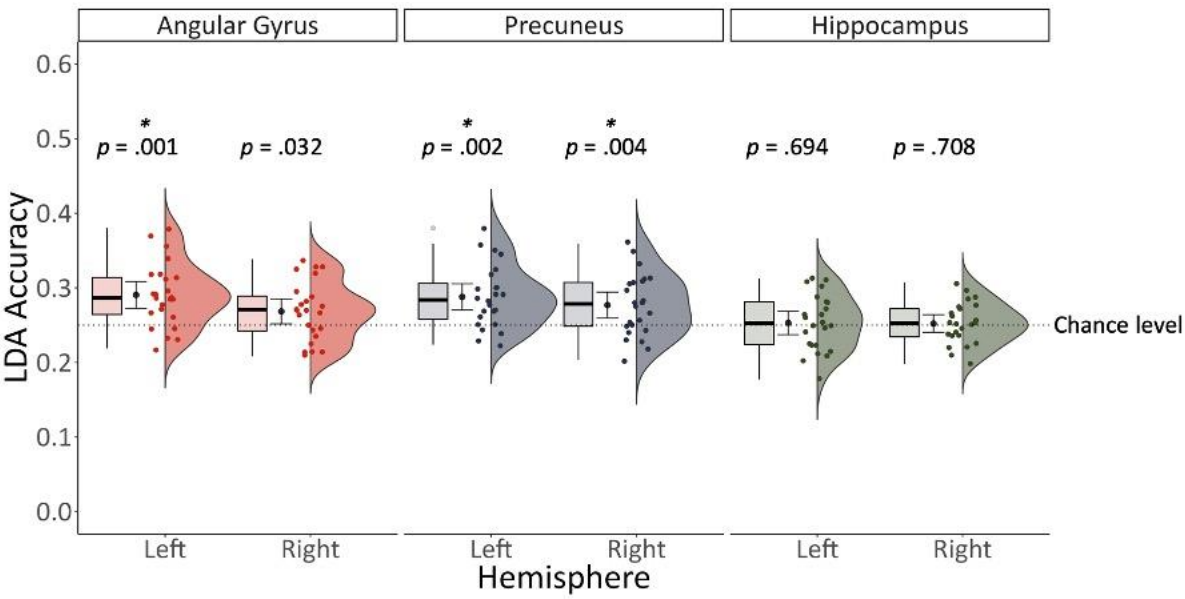

Figure 8. Decoding accuracy predicting the interaction of visual perspective and embodiment was significantly greater than chance in the left angular gyrus, left precuneus, and right precuneus. ⊥ = mean decoding accuracy +/- 95% confidence interval.

Classifier Accuracy Per Condition. For ROIs where neural activity significantly predicted embodiment or the interaction of embodiment and visual perspective across classes, we examined classifier accuracy per class to investigate whether an ROI contained more information related to one class, or whether classes were equally represented. For the analysis predicting embodiment from patterns of neural activity, decoding accuracy was equal between the sync (*M* = .53, *SD* = .05) and async (*M* = .53, *SD* = .05) classes in the left angular gyrus, *t*(23) = -0.18, *p* = .86, Cohen's d = -0.04. The same was true for the right precuneus, *t*(23) = -0.23, *p* = .82, Cohen's d = -0.05 (sync: *M* = .53, *SD* = .06; async: *M* = .53, *SD* = .05), and left precuneus, *t*(23) = 1.05, *p* = .30, Cohen's d = .18, (sync: *M* = .54, *SD* = .05; async: *M* = .53, *SD* = .06).

For the analysis predicting the interaction between embodiment and visual perspective using all four classes from patterns of neural activity in the left angular gyrus, there was no difference in classifier accuracy between the classes (in-body sync: *M* = .28, *SD*

= .07; in-body async: *M* = .31, *SD* = .09; out-of-body sync: *M* = .29, *SD* = .06; out-of-body async: *M* = .29, *SD* = .07). There was no main effect of perspective ($F(1,23) = .07$, $p = .80$, $\eta^2 = .003$), embodiment ($F(1,23) = 1.20$, $p = .13$, $\eta^2 = .05$), or their interaction ($F(1,23) = 2.10$, $p = .16$, $\eta^2 = .08$). There was also no difference in classifier accuracy between classes in the left precuneus (in-body sync: *M* = .28, *SD* = .08; in-body async: *M* = .30, *SD* = .09; out-of-body sync: *M* = .27, *SD* = .04; out-of-body async: *M* =.30, *SD* = .08). There was no main effect of perspective ($F(1,23) = .01$, $p = .93$, $\eta^2 = .004$), embodiment ($F(1,23) = 1.88$, $p = .18$, $\eta^2 = .08$), or their interaction ($F(1,23) = .06$, $p = .81$, $\eta^2 = .03$). Similarly, classifier performance was equal across classes in the right precuneus (in-body sync: M = .28, SD = .08; in-body async: M = .28, SD = .07; out-of-body sync: M = .26, SD = .07; out-of-body async: M = .28, SD = .07). There was no main effect of perspective ($F(1,23) = .27$, $p = .61$, $\eta^2 = .01$), embodiment ($F(1,23) = 1.11$, $p = .30$, $\eta^2 = .05$), or their interaction ($F(1,23) = .48$, $p = .50$, $\eta^2 = .02$).

Whole-brain searchlight analyses. The whole brain searchlight analyses did not reveal any regions where patterns of activity could decode visual perspective, embodiment, or the interaction of the two after corrections for multiple comparisons ($p_{FWE} < .05$).

Taken together, the decoding results revealed that visual perspective could not be decoded in any of the ROIs. In contrast, embodiment as well as the interaction between embodiment and visual perspective could be decoded from patterns of activity in the left angular gyrus and bilateral precuneus. Classifier accuracy was equal across classes, suggesting that there was no bias in decoding performance according to condition.

Discussion

The present study sought to understand how fundamental aspects of bodily selfhood, namely feelings of embodiment (i.e., self-location and body ownership) and visual perspective (i.e., in-body perspective, out-of-body perspective), experienced during the encoding of naturalistic events influence how that event is later represented in brain regions core to memory retrieval. Targeted region-of-interest multivariate analyses revealed that the left angular gyrus and bilateral precuneus contained information regarding the strength of embodiment at encoding and the interaction between embodiment and visual perspective during retrieval. In contrast, no region was found to represent visual perspective on its own, separated from embodiment. The results suggest that feelings of embodiment initially present during encoding are the predominant feature stored in posterior parietal memory traces for past events, while visual perspective is represented as a secondary, related component of bodily selfhood. The neuroimaging results are linked to our experimental manipulations of embodiment and visual perspective, rather than mediated by indirect influences in memory performance and subjective re-experiencing, as there were no initial differences between the conditions in memory accuracy, vividness, emotional intensity, or perceived memory accuracy. The visual perspective an event was encoded from determined the perspective at retrieval, which is consistent with previous literature (Bergouignan et al., 2022: Iriye & St. Jacques, 2021). Both immediately after encoding and during in-scanner retrieval, memories formed from an in-body perspective were retrieved from an in-body perspective, and memories formed from an out-of-body perspective were retrieved from an out-of-body perspective. Further, the interaction of visual perspective and embodiment during encoding influenced post-scanning memory accuracy. After repeated retrieval, cued recall accuracy was higher for memories encoded

from an embodied in-body perspective, compared to an embodied out-of-body perspective. This finding is consistent with previous reports that disrupting feelings of bodily selfhood is linked to deficits in episodic memory (Bergouignan et al., 2014; Bréchet et al., 2018, 2019; b, 2022).Together, the results reveal how the feeling of being located within and experiencing the world from the perspective of one's own body determines our ability to accurately remember details of past events, the visual perspective they are re-experienced from at retrieval, and how past events are represented in brain regions essential for creating unified, cohesive mental scenes based on egocentric reference frames during remembering.

Patterns of activity in the left angular gyrus contained information related to embodiment, and the interaction between embodiment and visual perspective. The current results are consistent with theories that the angular gyrus combines multisensory aspects of memories within a unified, egocentric (i.e., representing self-to-object relationships) scaffold, which enables subjective reliving during retrieval (Bonnici et al., 2016, 2018; Ciaramelli et al., 2010b; Yazar et al., 2014, 2017). The angular gyrus, especially in the left hemisphere, is a "convergence zone" where multiple streams of information from different modalities are integrated (Seghier, 2023). Previous research has shown that the multisensory information integrated in this region includes visual and tactile signals related to bodily selfhood. For example, trial-by-trial fluctuations in the left angular gyrus activity predict the emergence of the feeling of illusory ownership over a limb (Chancel et al., 2022). Further, patterns of activity in the left angular gyrus present during the encoding of an immersive event reflect strong versus weak body ownership and are reinstated more during the retrieval of memories encoded with strong body ownership and high vividness (Iriye et al., 2023). Additionally, a meta-analysis found that bilateral angular gyrus is implicated in mediating both feelings of bodily selfhood and episodic autobiographical memory (Bréchet

et al., 2018). Thus, the results of the present study align with previous research identifying the angular gyrus as a hub of multisensory integration leading to feelings of embodiment within memories of past events.

At the same time, the present study offers novel insights into how visual perspective is represented in the angular gyrus. Specifically, we show that visual perspective is intertwined with feelings of embodiment in memories of past events such that we could only decode the visual perspective associated with a given memory when also considering the level of embodiment experienced during encoding. Earlier investigations that have manipulated either visual perspective or embodiment, but not both, miss a fundamental component of the information stored in this region. For example, previous research has argued that the angular gyrus is involved in establishing a first-person perspective in a mental scene, enabling subjective remembering during retrieval (Bonnici et al., 2016; 2018; Ciaramelli et al., 2010; Yazar et al., 2017). Specifically, continuous theta burst stimulation applied to the left angular gyrus reduces the tendency to experience memories from an in-body perspective, demonstrating the causal role of this region in in creating a unified first-person perspective during retrieval. This account is consistent with neuropsychological evidence demonstrating that disrupting angular gyrus activity is correlated with the occurrence of out-of-body experiences (Blanke et al., 2004; Blanke et al., 2002; Ionta et al., 2011), and that lesions here reduce first-person perspective imagery during spatial 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 the angular gyrus represents both in-body and out-of-body perspectives without bias (i.e., classifier performance was equal across experimental conditions) according to embodiment

experienced during encoding. This finding suggests the angular gyrus is sensitive to differences between both types of visual perspectives and the bodily feelings elicited 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 previously reported (St. Jacques et al.., 2017). Thus, the present study refines current conceptions of egocentric representations within the angular gyrus by demonstrating that this region represents information related to both in-body and out-of-body visual perspectives integrated with feelings of embodiment during memory retrieval. By explicitly manipulating visual perspective alongside feelings of embodiment in the present study, we reveal that information linked with visual perspective in memories is inextricably tied with the feelings of body ownership and self-location initially experienced during encoding. These findings provide a more complete account of the role of the angular gyrus in memory for past events.

Like the angular gyrus, patterns of activity in the precuneus during memory retrieval also reflected embodiment at encoding, and the interaction between embodiment and visual perspective. Evidence for the role of the precuneus in bodily selfhood has only recently emerged. Lyu and colleagues (2023) observed that electrically stimulating both the left and right anterior precuneus led to feelings of dissociation from participants' physical bodies. Iriye and colleagues (2024) found that the right posterior precuneus encodes memories differently for events involving strong compared to weak body ownership, and that memory reinstatement during retrieval is greater for memories with strong body ownership and high vividness. Together with the results of the present study, these findings provide early evidence that the precuneus tracks embodiment as an event is formed, which influences the how bodily self-hood is represented during memory retrieval.

The precuneus is often associated with the ability to adopt a specific visual perspective in a memory or mental scene (Eich et al., 2009b; Freton et al., 2014b; Grol et al., 2017; Iriye & St. Jacques, 2020) and elaborate upon its visual details (Daselaar et al., 2008; Fuentemilla et al., 2014; Gardini et al., 2006; Söderlund et al., 2012). However, we observed that information related to visual perspective could only be detected when also including information connected to embodiment at encoding. Visual perspective on its own, separated from embodiment, could not be decoded from precuneus activity. This finding implies that previous studies that have investigated visual perspective in memory may also inadvertently been probing associated changes in embodiment (i.e., self-location, body ownership) that come with adopting a given visual perspective in memory. Moreover, previous results of the involvement of the precuneus during the instantiation of visual perspective in mental scenes can be explained by differing demands related to shifting between visual perspectives (St. Jacques et al., 2017; 2018), and manipulating images within an egocentric framework (Byrne et al., 2007). Supporting this idea, St. Jacques, Szupunar, and Schacter (2017) demonstrated involvement of the posterior parietal cortex (i.e., precuneus and angular gyrus) when participants were asked to actively shift their visual perspective during memory retrieval from a dominant in-body perspective to an observer perspective. Moreover, they found that the degree of precuneus involvement when shifting visual perspective also predicted the degree of reductions in emotional intensity during retrieval, as well as subsequent changes in the dominant visual perspective of autobiographical memories. 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 et al., 2018). These results 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 et al. ,2007). Such processes may be recruited more when people adopt an out-of-body perspective during retrieval, which is more likely to require updating internal representations of the world 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 perspective 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 in-body and out-of-body perspectives in previous investigations (Grol et al., 2017; Iriye & St. Jacques, 2020; St. Jacques et al., 2017; 2018). Future research that directly manipulates demands placed on mental transformation processes required to instantiate novel in-body and out-of-body perspectives in a mental scene is an important next step in elucidating the role of the precuneus in memory retrieval.

Turning to the hippocampus, we did not find activity in this region predicted visual perspective, embodiment, or their interaction during memory retrieval. Previous research has found delayed activation of the left posterior hippocampus when retrieving memories for events encoded from an out-of-body compared to in-body perspective, which coincided with reductions in vividness and impaired memory for episodic details during retrieval (Bergouignan et al., 2014). Further, bilateral hippocampal activity during encoding distinguishes between memories being formed with strong versus weak body ownership, which is then reactivated to a greater degree during the retrieval of memories formed with

strong body ownership and high vividness (Iriye et al., 2024). Conflicting results between these two previous studies and the present study may be due to reduced durability of memory traces for events encoded from an out-of-body perspective. Bergouignan and colleagues (2014) found that memory accuracy and vividness were lower for events encoded from an out-of-body relative to in-body perspective. In the present study, immediate memory performance and subjective re-experiencing was equated between conditions by repeating the word games several times and asking participants to retrieve mental images of each game immediately after encoding. Iriye and St. Jacques (2021) found that the durability of out-of-body perspective ratings decreased over time, further suggesting that memory traces for out-of-body events are less stable over time. Iriye and colleagues (2024) manipulated body ownership, but not visual perspective, and did not observe differences in memory accuracy between conditions. Together, these studies suggest that out-of-body perspectives in particular may lead to less durable memory traces, which may contribute to changes in the involvement of the hippocampus. Regardless, the results of the present study underscore that bodily selfhood is integrated within memories of past events in regions outside of the medial temporal lobes and in posterior parietal cortex (i.e., the angular gyrus and precuneus).

Our results generate original insights into clinical reports of disorders exhibiting both abnormal body experiences and memory impairments. For example, disruptions in own-body perception are a core symptom of schizophrenia (Costantini et al., 2020; Schultze-Lutter, 2009), which can involve a weakened sense of body ownership and blurred boundary between self and the external world (Di Cosmo et al., 2018; Thakkar et al., 2011; van der Weiden et al., 2015). At the same time, schizophrenia is often associated with impairments in episodic memory, which have been linked to an inability to bind object level information

with spatial contextual information during encoding (Aleman et al., 1999; Brébion et al., 1997; Rushe et al., 1999; Talamini et al., 2010). Deficits in remembering verbally presented information, such as the word games in the present study, during childhood are also a key predictor of the development of schizophrenia (Erlenmeyer-Kimling et al., 2000). The paradigm of the present study allows for the induction of abnormal body experiences (i.e., weakened body ownership, shifts in self-location, and out-of-body perspectives) in healthy individuals. Using this innovative paradigm that creates highly realistic, immersive memories tightly controlled in a lab setting, we show that encoding events from an out-of-body perspective leads to reduced recall of event details compared to when events are encoded from a perspective within one's body, which mimics reported impairments in episodic memory in patients with schizophrenia. Previous models of impaired binding processes during memory encoding in schizophrenia have focused on connectivity within medial temporal lobe regions (Talamini et al., 2005, 2010; Talamini & Meeter, 2009). However, our results indicate that posterior parietal regions including the angular gyrus and precuneus contain information related to embodiment and visual perspective that are critical to building egocentrically defined reference frames that facilitate memory retrieval, and should be considered in medio-temporal lobe models of schizophrenia.

In sum, the present study combines 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. Patterns of activity in the left angular gyrus and bilateral precuneus during the retrieval of lifelike events predicted feelings of embodiment experienced during encoding, and the visual perspective an event was encoded from considering embodiment. Ultimately, this line of research elucidates how an elusive, multifaceted sense of bodily self becomes incorporated within

memories of the personal past to structure higher levels of selfhood contingent on autobiographical memories. Here, we highlight brain regions that may be implicated in mediating episodic memory impairments reported in disorders involving depersonalization and dissociation, such as schizophrenia (Borda & Sass, 2015; Prebble et al., 2013; Sierra & David, 2011).

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