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Bodily self-consciousness as a framework to link sensory information and self-related components of episodic memory: behavioral, neuroimaging, and clinical evidence

Nathalie Heidi MEYER

Bodily self-consciousness as a framework to link sensory information and self-related components of episodic memory: Behavioral, neuroimaging, and clinical evidence

Abstract

The recollection of sensory information and subjective experience related to a personal past event depends on our episodic memory (EM). At the neural level, EM retrieval is linked with the reinstatement of hippocampal activity thought to recollect the sensory information experienced and stored in the cortex. At encoding, the sensory information also includes many bodily cues (i.e., touch, proprioception). Such integrated bodily signals are the basis of a sensorimotor form of self-consciousness called bodily self-consciousness (BSC). BSC consists of subjective experiences like the sense of ownership, first-person perspective, and the sense of agency, recruiting a distributed neural system consisting of premotor (PMC), supplementary motor (SMA), and posterior parietal regions. However, although both BSC and EM rely on the integration of sensory stimuli, the neural mechanism associating BSC and EM are still not known.

In my thesis, I designed a new experimental procedure using virtual reality (VR) and motion tracking to investigate the behavioral and neural correlates of BSC, EM, and their interactions. I fully adapted the procedures to fMRI in order to test the impact of BSC manipulation at encoding on EM retrieval and its subjective components. The first part of my thesis investigated how different levels of BSC (visuomotor and perspectival congruency) during encoding impacted EM (Study 1) and the subjective re-experience of the memory called autonoetic consciousness (ANC; Study 2). In Study 1, I found that hippocampal reinstatement was enhanced and coupled with key BSC areas (PMC, SMA) only for preserved BSC characterized by visuomotor and perspectival congruency. Study 2 showed that the strength of recollection correlated with the strength of the subjective experience at encoding only under visuomotor and perspectival congruency. This relationship between ANC and BSC was mediated by the insula, a structure related to BSC and also linked with emotions in the EM field.

In the second part of my thesis, I investigated the paradigm used in Studies 1 and 2 in clinical populations presenting damage to the medial temporal lobe (Study 3) or cortical areas (Study 4). In Study 3, I tested a rare case of amnestic patient with bilateral damage to the hippocampal complex. Despite preserved BSC, the patient showed a decreased EM when encoded under a BSC characterized by visuomotor and perspectival congruency. In Study 4, I tested whether damage to frontal cortex, including PMC, in motor stroke patients alters the impact of BSC state in EM. Preliminary results indicated that memory performance for scene encoded under visuomotor and perspectival congruency was not enhanced in stroke patients with impaired BSC. Finally, in the last part of my thesis, I discuss the importance of VR technology in the study of BSC and what to improve in VR aesthetics to boost BSC effects in future studies.

In summary, I designed a new experimental protocol using VR and motion tracking to investigate the impacts of BSC and its related subjective experience on EM. I adapted the

design to fMRI to investigate the neural correlates of the association of these two processes. I linked these results in light of a rare case of an amnestic patient with a specific EM deficit and a group of motor stroke patients with lesions involved in BSC processes. My thesis contributes to linking sensory information processing, self-consciousness, and EM within a common framework: BSC.

Keywords: bodily self-consciousness, autobiographical memory, episodic memory, autonoetic consciousness, virtual reality, functional magnetic resonance imaging.

Résumé

Le souvenir d'informations sensorielles et d'expériences subjectives liées à un événement personnel passé dépend de notre mémoire épisodique (« episodic memory » ; EM). Au niveau neuronal, la récupération de la mémoire épisodique est liée à la réactivation de l'activité de l'hippocampe qui indexe le transfert des informations sensorielles vécues et stockées dans le cortex. Lors de l'encodage, les informations sensorielles comprennent également de nombreux signaux corporels (par exemple, le toucher, la proprioception). Ces signaux corporels intégrés sont à la base d'une forme sensorimotrice de conscience de soi appelée conscience de soi corporelle (« bodily self-consciousness » ; BSC). La BSC consiste en des expériences subjectives telles que le sentiment de possession du corps (« body ownership ») , la perspective à la première personne et le sentiment d'agentivité (« sense of agency »), recrutant un système neuronal distribué composé de régions prémotrices (PMC), motrices supplémentaires (SMA) et pariétales postérieures. Cependant, bien que la BSC et la EM reposent toutes deux sur l'intégration de stimuli sensoriels, les mécanismes neuronaux associant la BSC et la EM ne sont toujours pas connus.

Dans ma thèse, j'ai conçu une nouvelle procédure expérimentale utilisant la réalité virtuelle (« virtual reality » ; VR) et le suivi du mouvement pour étudier les corrélats comportementaux et neuraux de la BSC, de la EM et de leurs interactions. J'ai entièrement adapté les procédures à l'IRMf afin de tester l'impact de la manipulation de la BSC lors de l'encodage sur la récupération de l'EM et ses composantes subjectives. La première partie de ma thèse a examiné comment différents niveaux de BSC (congruence visuomotrice et perspectivale) pendant l'encodage ont eu un impact sur la EM (étude 1) et la réexpérience subjective du souvenir appelée conscience autonoétique (« autonoetic consciousness » ; ANC ; étude 2). Dans l'étude 1, j'ai trouvé que la réintégration hippocampique était renforcée et couplée avec les zones clés de la BSC (PMC, SMA) uniquement pour la BSC préservée caractérisée par la congruence visuomotrice et perspectivale. L'étude 2 a montré que la force du souvenir était corrélée à la force de l'expérience subjective lors de l'encodage uniquement en cas de congruence visuomotrice et perspectivale. Cette relation entre ANC et BSC était médiée par l'insula, une structure liée à la BSC et également liée aux émotions dans le champ EM.

Dans la deuxième partie de ma thèse, j'ai étudié le paradigme utilisé dans les études 1 et 2 dans des populations cliniques présentant des lésions du lobe temporal médian (étude 3) ou des zones corticales (étude 4). Dans l'étude 3, j'ai testé un cas rare de patient amnésique avec des dommages bilatéraux au complexe hippocampique. Malgré une BSC préservée, le patient a montré une EM diminuée lorsqu'elle était encodée sous une BSC caractérisée par une congruence visuomotrice et perspectivale. Dans l'étude 4, j'ai testé si les dommages au cortex frontal, y compris le PMC, chez les patients ayant subi un accident vasculaire cérébral moteur modifient l'impact de l'état de la BSC sur la EM. Les résultats préliminaires ont indiqué que la performance de la mémoire pour les scènes encodées dans le cadre d'une congruence visuomotrice et perspectivale n'était pas améliorée chez les patients victimes d'un AVC dont la BSC était altérée. Enfin, dans la dernière partie de ma thèse, je discute de l'importance de

la technologie VR dans l'étude de la BSC et de ce qu'il faut améliorer dans l'esthétique VR pour stimuler les effets de la BSC dans les études futures.

En résumé, j'ai conçu un nouveau protocole expérimental utilisant la VR et le suivi du mouvement pour étudier les impacts de la BSC et de l'expérience subjective qui lui est associée sur l'EM. J'ai adapté la conception à l'IRMf pour étudier les corrélats neuronaux de l'association de ces deux processus. J'ai relié ces résultats à la lumière d'un cas rare d'un patient amnésique présentant un déficit spécifique de l'EM et d'un groupe de patients victimes d'un accident vasculaire cérébral moteur présentant des lésions impliquées dans les processus de BSC. Ma thèse contribue à relier le traitement des informations sensorielles, la conscience de soi et l'EM dans un cadre commun : BSC.

Mots-clés: conscience de soi corporelle, mémoire autobiographique, mémoire episodique , conscience autonoétique, réalité virtuelle, imagerie par résonance magnétique fonctionnelle.

Acknowledgments

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Abbreviations

1PP	First-person perspective		**RVLT**	Rey Auditory Verbal Learning Test
ANC	Autonoetic consciousness		**SMA**	Supplementary motor area
BSC	Bodily self-consciousness		**SoA**	Sense of agency
dPMC	Dorsal premotor cortex		**SoO**	Sense of ownership
EAM	Episodic autobiographical memory		**TMT**	Trail Making Test
EAMI	Episodic autobiographical memory Interview		**TTT**	Trace Transformation Theory
EM	Episodic memory		**VR**	Virtual reality

EPI Echo planar imaging

ERS Encoding-recognition similarity

FAB Frontal Assessment Battery

FBI Full-body illusion

FDR False discovery rate

fMRI Functional magnetic resonance imaging

FWE Family wise error

GLM General linear model

HMD Head-mounted display

MCQ Memory Characteristics Questionnaire

MNI Montreal Neurological Institute space

mPFC Medial prefrontal cortex

MPRAGE Magnetization-Prepared Rapid Acquisition with Gradient Echo

MTG Middle temporal gyrus

MTT Multiple Trace Theory

rs Resting-state

RSA Representational similarity analysis

1. General introduction

1.1 Motivation

In our everyday life, we receive thousands of sensory inputs from external stimuli, giving rise to a palette of subjective experiences associated with specific moments of our lifetime. How can our brain reconstruct the subjective experience of events encoded, sometimes several years before we recollect them? And why do I remember so well the coffee I drank on the terrasse of my favorite restaurant next to my home two weeks ago, but I cannot remember what I ate today? Or in other terms, how does the subjective experience related to an event impact our memory of these same events? At the intersection between self-consciousness and EM as well as sensory-motor information processing - these questions motivated the present thesis.

When I remember the coffee I drank two weeks ago, I remember that I was sitting on a chair outside, and drinking the delicious coffee warmed me up as it was cold outside. I also remember thinking about what I should add to my thesis discussion to make it more interesting. In other words, when remembering this coffee, I recollect a lot of sensory information and thoughts related to what I perceived during the event, which led to the related subjective mental states. To perform this task, I am using what is called episodic memory (EM).

EM is at the core of the questions asked above and is defined as a form of long-term memory that involves the recollection of sensory and contextual details of events personally experienced in the past (Tulving, 1985, 2002). One of the central components of EM is autonoetic consciousness (ANC). At the junction between memory and self-consciousness, ANC is defined as the ability to mentally relive a past event and recollect its related subjective experience (Markowitsch & Staniloiu, 2011; Piolino et al., 2006; Tulving, 1985; M. A. Wheeler et al., 1997). This implies attributing a given event to something that was *personally* experienced and *consciously* recollecting the information related to this past experience. Hence, the definition of ANC links both the self and memory within a common framework. The sensory context is of critical importance as well, because the sensory information acts both as a cue to facilitate the retrieval of events (Brunel et al., 2009; Sorokowska et al., 2022) and forms the episodic content of a memory.

Most past research has focused on the role of auditory and visual stimuli and how their related brain activity is reinstated during the retrieval of EM (Bosch et al., 2014; Wheeler, 2000). However, the role of the observer's body in this context and the related sensory inputs have not received a lot of interest in the scientific community. Importantly, the body provides a rich substrate of sensory stimuli during encoding. These include tactile, proprioceptive, vestibular, and visual cues about the body (i.e., the observer's hand in the visual field) that are further

integrated with motor signals from the observer's movements. Moreover, recent research has shown that beyond the relevance of bodily cues for the sensory context of EM, the integration of multisensory and sensorimotor bodily signals from the observer's body is a fundamental brain system involved in self-consciousness, especially bodily self-consciousness (BSC; Blanke, 2012; Blanke et al., 2015; Park & Blanke, 2019). BSC can be defined as a pre-reflective, non-cognitive form of self-consciousness based on multisensory and sensorimotor signals. BSC is fundamental for the subjective experience of a unitary self, consisting of four different components of BSC. Sense of agency (SoA, the feeling of being in control of one's own body), sense of body-ownership or self-identification (the feeling that the body belongs to oneself), first-person perspective (1PP; the experience of observing the world and its objects from the perspective of the body) and sense of self-location (the feeling that the "self" is centered in space, around the body; Blanke, 2012; Blanke et al., 2015).

What is the role of the bodily context and especially BSC during the encoding of an event for the recollection of EM and ANC? My thesis aimed to address this question, with a particular focus on the neural correlates and related mechanisms that link sensorimotor aspects of BSC and EM. The present work is based on the shared multisensory and sensorimotor integration processes reported in both BSC and EM studies (Blanke et al., 2015; Brunel et al., 2009; Park & Blanke, 2019; Wheeler, 2000). Recent studies showed that encoding an event under a change of perspective or sense of ownership – both key components of BSC – modulates EM (Bergouignan et al., 2014; Bréchet et al., 2019; Gauthier et al., 2020; Iriye & Ehrsson, 2022). Neuroimaging studies provided evidence that such manipulations modulated the hippocampal activity and its functional connectivity with the parahippocampus (Bergouignan et al., 2014; Gauthier et al., 2020), therefore linking BSC manipulation with memory-related brain regions (Kesner, 1980; Moser & Moser, 1998). Moreover, EM and BSC share some common neural substrates, such as angular gyrus and precuneus (Blanke & Arzy, 2005; Bréchet et al., 2018; Cabanis et al., 2013; Linden et al., 2017; Trimble & Cavanna, 2008).

Based on this behavioral and neuroimaging evidence, in my thesis, consisting of a series of 5 studies (chapters 2 to 4), I focused on how the manipulation of the SoA, a key component of BSC, influences EM, by using a variety of behavioral, technological, neuroimaging, and clinical methods. In the last chapter of my thesis, I discuss these findings in light of episodic autobiographical memory, the episodic component of autobiographical memory.

The following section summarizes the necessary background on EM and BSC that motivated the present thesis.

1.2 Episodic memory

Long-term declarative memory is a type of memory that involves encoding, storage, and retrieval of memory about general knowledge (semantic memory) and personal events (episodic memory; EM; Lum & Conti-Ramsden, 2013; Tulving, 1972). "Bern is the capital of Switzerland" is an example of semantic memory. While semantic memory is not necessarily dependent on its encoding context (although I remember that Bern is the capital of Switzerland, I do not know when or who taught me that), EM, on the other hand, contains the memory of personally experienced events in a unique spatiotemporal context ("The coffee I drank two weeks ago was delicious").

Classically, EM is tested by asking a subject to learn a list of items (for example, a list of words; Crossen et al., 1987) and further test the memory ability of context retrieval. Several tests can be used to test the participant's episodic retrieval ability. The participant can undergo a free recall test where the subject has to list all previously presented items without additional cues (Earhard, 1967; Rundus, 1971). Another way to measure EM is via a recognition task, in which the subject has to indicate which items were presented from a list of both learned items but also new items (Anderson & Bower, 1972; Tulving & Wiseman, 1975). Finally, another classical retrieval test consists of giving a cue (for example, the three first letters of a word) and asking the subject to complete the retrieval (Earhard, 1967; Tulving & Osler, 1968). Free recall, recognition, and cued recall are different ways to measure EM, are easy to implement, and have been employed in innumerous studies. However, they have at least two major drawbacks: they are not entirely specific to EM as they involve semantic memory system as well (Pause et al., 2013) and do not test memory under ecological conditions: for example, when I remember the coffee I drank two weeks ago, I can remember the cold weather, the warmth of the coffee, the color of the chair on which I was sitting and the thought I had about the writing of my discussion. The recollection of this memory is most likely much richer in terms of sensory, perceptual and emotional details than a list of words (Pause et al., 2013).

The increased use of virtual reality (VR) in the field of cognitive neuroscience (Pan & Hamilton, 2018; Skurla et al., 2022) facilitated the investigation of several brain functions in ecologically valid and controlled conditions (Pan & Hamilton, 2018; Sanchez-Vives & Slate, 2005; Smith, 2019). VR is of particular interest for research investigating EM as it allows to create scenarios that are richer and closer to what is experienced in real life (i.e., compared to the encoding of a list of words), while keeping a close control on the encoding context. VR has allowed passing from encoding a list of words to encoding objects in scenes (Davis et al., 1999; Gamberini, 2000; Krokos et al., 2019).

VR also boosted the research on the sensory context of EM by comparing the effect of encoding under unisensory modality (for example visual) versus multisensory modality (for example visuoauditory). Researchers demonstrated improved memory performance and faster reaction times for memories encoded with multisensory modalities compared to

unisensory (Andreano et al., 2009; Dinh et al., 1999; Tortell et al, 2007). For example, one study asked participants to navigate in a virtual room associated with different levels of auditory quality (high, low, or no audio) and containing different objects. The study reported better recognition performance in the high audio quality scenes compared to the no audio scenes (Davis et al., 1999). VR can also test the effect of motor involvement on memory. In one study, participants were asked to navigate a virtual city while immersed in a virtual car. They navigated either with complete navigation control (active condition), no control (passive condition) or under "planning condition" (they could plan the whole drive but could not drive during the navigation). The study showed that active and planning conditions gave rise to better recognition performance than the passive condition (Plancher et al., 2013; Smith, 2019).

Autonoetic consciousness

One of the specific features of EM is the ability to mentally re-experience an event from the past. This feature is called autonoetic consciousness (ANC) and has been argued to be at the core of the link between EM and self-consciousness. ANC enables the recollection of the subjective experience linked to an event (Markowitsch & Staniloiu, 2011; Tulving, 1985; M. A. Wheeler et al., 1997). For example, when recollecting the coffee smell and warmth on my lips and in my mouth as well as the coldness of winter before arriving at the coffee shop two weeks ago, I am using ANC.

State-of-the-art procedures to measure ANC and the related subjective aspect of EM include two types of tests. The "remember-know" paradigm is a standard test to measure memory recollection (A. Gardiner et al., 2001; Tulving, 1985). In this paradigm, a "remember" answer is linked with the recollection of the event (the recollection of the subjective experience lived at encoding). A "know" answer refers to a feeling of familiarity without necessarily remembering the event or item encoded. The "remember" answer is generally associated with ANC, while the "know" answer is related to general knowledge and semantic processing (A. Gardiner et al., 2001). Although this test is still widely used today, it assesses the recollection of memory using binary answers ("Remember" versus "know"), therefore giving fewer details on the strength of recollection of different aspects of the re-experience. Numerous questionnaires were created to measure ANC in greater detail by measuring the strength of recollection and re-experience of memory with ordinal scales; this enabled a better precision than the binary choice provided by the "remember-know" paradigm (Irish, 2008; Irish et al., 2011; M. K. Johnson et al., 1988). These tests use several subquestions to measure different aspects of the quality of the recollection. The perspective at retrieval is often included in these questionnaires, as it has been shown that it can differ depending on the strength and the age of the memory (Nigro & Neisser, 1983; St. Jacques et al., 2017). Emotional reliving, vividness, and re-experiencing are other important categories that are also included in questionnaires to test ANC. These different categories enabled disentangling different ANC aspects. For example, in schizophrenia patients, ANC for emotional events is reduced, and ANC is usually

associated with less re-experience from a 1PP compared to control group (Neumann et al., 2007; Potheegadoo et al., 2013).

Autobiographical memory

When memory is integrated as part of one's personal history, it becomes an autobiographical memory (Piolino et al., 2003; Tulving, 1985). If in a few years, I can still remember the delicious coffee I tasted two weeks ago at the particular terrasse and city, this memory would have been integrated into my personal history and become part of my autobiographical memory. Autobiographical memory is one of the core aspects of human cognition and is thought to contribute to the maintenance and construction of personal identity (Allebone et al., 2015; Markowitsch & Staniloiu, 2011; Piolino et al., 2006). Autobiographical memory includes knowledge related to oneself (Piolino et al., 2003; Tulving, 1985). Tulving proposed to divide autobiographical memory between a semantic component (semantic autobiographical memory) which contains the general self-knowledge and an episodic component (Episodic autobiographical memory; EAM), which comprises the recollection of a specific experience in its unique spatiotemporal context (A. Conway et al., 2001; Tulving, 1985, 2002). "I was born in Lausanne" is an example of semantic autobiographical memory, a knowledge about myself that I cannot re-experience. On the opposite, "the day I received my driver's license" , is an example of EAM, a memory in a unique spatiotemporal context, personally experienced, for which I can consciously recollect its subjective aspects and sensory information and which is part of my personal history. According to this definition, what distinguishes an EM from an EAM, is that a specific EM has to be integrated into the personal history to become EAM.

This definition makes the study of EAM challenging. One of the difficulties is the lack of control over the events: the experimenter is not present at the time of encoding of an EAM; therefore, EAM studies lack objective material to evaluate the accuracy of EAM-related retrieval. To overcome this issue, some studies gave cameras to participants who wore them for several days. The camera was programmed to take pictures at random moments of the day. Researchers could then use the content of the picture to ask about the events that happened and therefore have a way to measure memory accuracy for real life events (Allé et al., 2017; Hodges et al., 2011). Other studies have created real-life events such as a museum tour to control the encoding of a scene and test EAM later (St. Jacques & Schacter, 2013).

Although providing objective material to assess EAM accuracy, it is hard to control for the difference of sensory parameters and salience of the event with these studies. For example, two participants wearing a camera for a week could have very different EAM based on the richness of the sensory, perceptual, and emotional stimuli related to the events they lived during the week. Similarly in the museum tour, it is difficult to account for the variability of events that can happen during the museum, which could give rise to different EAM strengths. Accordingly, more recently, researchers have brought the encoding into the lab to enhance the control of these different parameters. For example, some studies have asked participants

to perform various short tasks in a lab and measured participants' EAM based on photographs from these laboratory events (Marcotti & St. Jacques, 2022).

Although gaining necessary controls, bringing EAM encoding in the lab also has some critical drawbacks. Specifically, it has the disadvantage of weakening the *autobiographical* component of the tested EM (since events encoded in the lab are controlled for many factors, they are usually less rich and less relevant for the participant than real life situations). However, it enables to improve the investigation of the behavioral and neural correlates linked to EAM and its related mechanisms as it allows to control for multiple parameters that could not be controlled when exploring EAM (e.g., control for the richness of perceptual details and emotional arousal across participants). Based on these studies, in my thesis I developed an approach that tested EM in immersive VR to get as close as possible to ecological encoding conditions and related the findings to EAM.

1.3 Neural substrate of EM recollection

Neural correlates of EM

One of the most widely accepted consensuses in the study of EM is the involvement of the hippocampus during encoding, storage and retrieval processes (Cutsuridis et al., 2010; Kesner, 1980). The hippocampus is part of the medial temporal lobe (**Figure 1a & 1c**) and can be divided into three subparts based on its cytoarchitecture: the three cornu ammonis regions (CA1, CA2, and CA3), the dentate gyrus (DG) and the subiculum (**Figure 1b**). Studies showed a distinction between encoding processes thought to be mediated by the DG, CA1 and CA2, and retrieval processes thought to be mediated by the subiculum (Eldridge et al., 2005). The hippocampus can also be divided along its anterior-posterior axis, into three subparts: the tail, body and head (Fanselow & Dong, 2010; Moser & Moser, 1998). Some studies propose distinct roles of each subdivision, where the posterior hippocampus is generally thought to mediate the recall of place and scene, and the anterior hippocampus the recall of objects and faces (Turk-Browne, 2019). Although the exact role of each of these divisions differs between studies, they all converge into the importance of hippocampus for EM formation and retrieval.
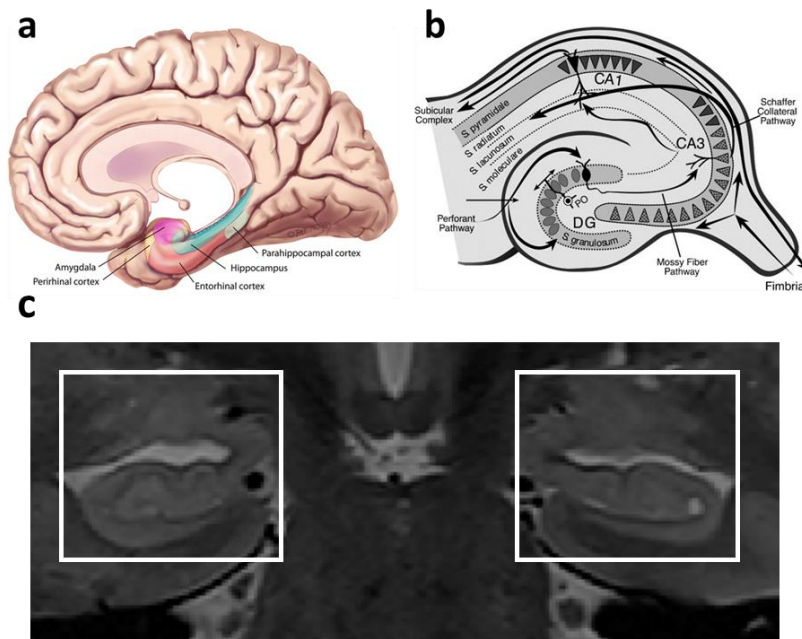
Figure 1. Different representation of hippocampus and its subdivision. (a) Sagittal view of medial temporal lobe, from Raslau et al., 2014. (b) Detailed view of the hippocampus From Harry & Lefevbre d'Hellencourt, 2003 (Harry & Lefevbre d'Hellencourt, 2003). (c) Coronal view of bilateral hippocampi (white squares) of a young healthy participant from a 7T MRI (image given by Campus Biotech, Geneva).

The medial temporal lobe, including the hippocampus and parahippocampal areas, was first thought to be sufficient to mediate EM encoding and retrieval, but evidence has accumulated to show that cortical areas also play an important role in EM (Moscovitch et al., 2016; Summerfield et al., 2006). Numerous studies reported prefrontal and parietal cortex activity during EM retrieval (Blum et al., 2006; Bonnici et al., 2018; Eichenbaum et al., 2007; Linden et al.,2017). Moreover, depending on the nature of the retrieval, different sensory brain regions have been observed as well, among which the most common are the visual and auditory cortex, as numerous studies used these sensory modalities to investigate EM (Bosch et al., 2014; Wheeler, 2000). Finally, the amygdala and insula are also typical brain regions involved in EM retrieval for memory with high emotional arousal (Dere et al., 2010; Hamann et al., 1999; Kensinger & Ford, 2020; Phelps, 2004).

Clinical reports of patients with retrograde amnesia helped to pinpoint the brain regions specifically involved in ANC, the conscious re-experience of an event. Piolino described the case of a patient with hypometabolism on the right ventral frontal lobe with deficit of EM, specifically in ANC (Piolino et al., 2003). Damage to the ventral frontal cortex leading to retrograde amnesia in EM was also detailed in the case of a patient with deficit in ANC for both events encoded before and after the damage (Levine et al., 1998). Lesions to the prefrontal and left hippocampus led to a similar deficit in another patient reported by Levine (Levine et al., 2009). Hippocampal lesions also accounted for deficit of re-experiencing EAM as observed in (Rosenbaum et al., 2008). Therefore, the prefrontal cortex and the hippocampus seem to play a critical role in ANC. This is further emphasized by several

empirical works testing healthy participants during free recall of autobiographical memory and reporting activation in the hippocampus and prefrontal cortex (Addis et al., 2004; McCormick et al., 2020; Ryan et al., 2001).

So how do these brain regions relate to each other in the context of EM? Although this question is not fully understood yet, part of the explanation is described in the next section.

The hippocampus-neocortical axis

The connection between the hippocampus and cortical areas is established through its structural connection with the entorhinal cortex. The hippocampus is considered at the top of the hierarchical organization of the medial temporal lobe (**Figure 2**), receiving only highly integrated neural signals from unisensory and multisensory areas, which were first passed through the parahippocampal complex and entorhinal cortex (Lavenex & Amaral, 2000; Shimamura, 2010; Shimamura & Wickens, 2009).

As multisensory and unisensory stimuli are integrated into the neocortical areas (Ghazanfar & Schroeder, 2006), theories explaining the recollection of EM attempted to link the hippocampus and medial temporal lobe with neocortical areas. One of the first theories to do so was the standard theory of memory consolidation (Squire, 1992; Squire et al., 2004). Based on clinical cases of patients with retrograde amnesia (i.e., with the remaining ability to retrieve early childhood memories), this theory suggested that the hippocampus is involved in the early stage of memory storage, after which the memory trace "migrates" to the neocortex and its retrieval become independent of the hippocampus (Squire, 1992; Squire et al., 2004). This theory was challenged by the emergence of the multiple trace theory (MTT), in which the hippocampus remains central for the retrieval of episodic memories but not for semantic memory, which can be retrieved directly with cortical brain regions regions ((Nadel et al., 2000). More recently, an updated version of the MTT was proposed, the Trace Transformation Theory (TTT), in which the posterior hippocampus and posterior neocortex link the contextual and perceptual details of the memory, while the global representation of memory is linked between the anterior hippocampus and the anterior neocortex (which contains the medial prefrontal cortex; mPFC). Critically, this theory proposes that the hippocampus and neocortical regions can be involved conjointly or independently depending on the nature and needs of the retrieval (Winocur & Moscovitch, 2011).

Neural reinstatement

A possible mechanism to explain how the hippocampus retrieves the sensory information stored in the cortex is through the reactivation of its encoding activity at retrieval, a process called reinstatement (Oedekoven et al., 2017). Numerous empirical studies have observed reinstatement of the medial temporal lobe such as in the perirhinal cortex, middle temporal gyrus, parahippocampus and hippocampus (Davachi, 2006; Eichenbaum et al., 2007; Liang & Preston, 2017; Pacheco Estefan et al., 2019; Staresina et al., 2013; Tompary et al., 2016; M. E. Wheeler & Buckner, 2004; Woodruff et al., 2005). But the medial temporal lobe is not the only

brain region to reinstate its encoding activity during retrieval. Reinstatement of cortical regions involved at encoding has also been described (Bosch et al., 2014; J. Johnson et al., 2013; Kahn et al., 2004; Nyberg et al., 2000; Staresina et al., 2013; Wheeler, 2000; M. E. Wheeler & Buckner, 2004; Woodruff et al., 2005; Xiao et al., 2017). For example, in the study of Wheeler (Wheeler, 2000), reactivation of the auditory cortex was detailed during the retrieval of encoded word-sound, even when the sound was not asked to be retrieved. Since then, a variety of cortical regions has been reported as being reinstated during EM retrieval, among which the posterior cingulate cortex, prefrontal cortex, lateral and medial parietal cortex (which includes angular gyrus and precuneus), as well as auditory, and visual cortex depending on the encoding context (J. Johnson et al., 2013; Kahn et al., 2004; Wheeler, 2000; M. E. Wheeler & Buckner, 2004; Woodruff et al., 2005).
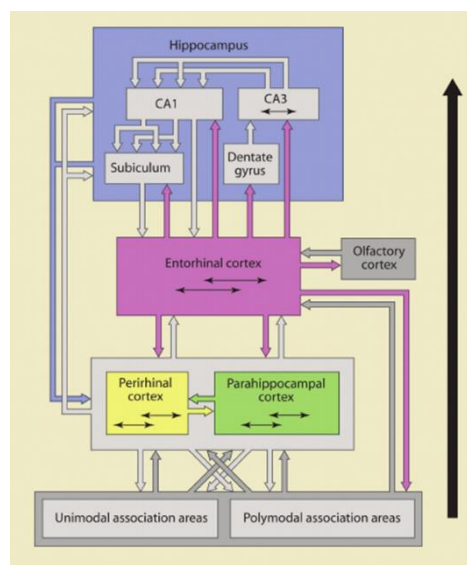
Figure 2. Organization of inputs received in the medial temporal lobe. Schema of the medial temporal lobe and its connection to neocortical areas, from Raslau et al. 2014.

Importantly, reinstatement of the hippocampus has been linked with cortical reinstatement (Staresina et al., 2013; Woodruff et al., 2005). Therefore some researchers have proposed that hippocampus reinstatement was necessary to reinstate the cortical regions involved in encoding and thus recollecting an event's experience. This was further supported by empirical evidence showing that cortical reinstatement was correlated with hippocampal reinstatement during EM retrieval (Danker et al., 2017; Gordon et al., 2014; Ritchey et al., 2013). Therefore, reinstatement is a possible neural mechanism to explain how the recollection of EM through the hippocampal-neocortical axis works.

1.4 Self, body, and bodily self-consciousness

Our body is present during the encoding of every event and can be seen as a scaffold that provides bodily-sensory and bodily-motor context of relevance for EM. Moreover, it has been shown that specific bodily signals are of key importance for self-consciousness. The self and self-consciousness can be separated into two main components: narrative-cognitive self-consciousness and minimal-bodily self-consciousness (Gallagher, 2000). The latter has been referred to as bodily self-consciousness (BSC) and is thought to provide an important biological system enabling the simplest form of self-consciousness (Blanke et al., 2015; Blanke & Metzinger, 2009; Ehrsson, 2007; Tsakiris et al., 2010). BSC is a form of lower-level self-consciousness arising from the multisensory and sensorimotor integration of bodily signals. It has been argued that the multisensory and sensorimotor integration of bodily signals gives rise to four main BSC elements, enabling the subjective experience of a unitary global sense of self, experienced within the body boundaries. These four key elements are the following: sense of ownership (the feeling that the body belongs to oneself), sense of agency (SoA, the feeling of being in control of one's body), first-person perspective (1PP, the experience to be directed at the world from a body-centered perspective) and self-location (the experience that the self is located within a spatial volume, most often co-located and centered around the person's body; Blanke et al., 2015; Blanke & Metzinger, 2009). Clinical observations first supported the investigation of BSC, with some cases of somatoparaphrenia (misattribution of one's own limb to someone else) in neurological patients following stroke (Baier & Karnath, 2008), out-of-body experiences in epileptic patients (Blanke & Castillo, 2007; Blanke & Mohr, 2005), as well as the loss of SoA in schizophrenia (Jeannerod, 2009).

Experimental manipulation of BSC

The study of BSC in healthy participants relies on the induction of a sensory mismatch that alters the report of subjective experience. The first breakthrough in laboratory-based BSC research was the rubber hand illusion (RHI; Botvinick, 1998), in which the experimenter strokes synchronously a rubber hand and the hand of a participant hidden outside of his/her field of view. The synchronous stroking triggers an altered sense of ownership (from one's own hand towards the rubber hand). The advance in VR technology in the last decades boosted research on BSC by allowing the study of its behavioral and neural correlates in healthy participants in controlled laboratory conditions using illusions that would be harder to induce in real life (Galvan Debarba et al., 2018; Lenggenhager et al., 2007; Moon et al., 2022; Sanchez-Vives & Slate, 2005; Tsakiris et al., 2010). One example is the usage of visuomotor mismatch that induces changes in SoA (David et al., 2008; Haggard, 2017; Haggard and Chambon, 2012), the feeling of being in control of one's body (Park & Blanke, 2019). Visuomotor mismatch can be achieved by imposing a delay between a movement performed by the participant and the movement displayed in the virtual environment. When the delay is

long enough (Haering & Kiesel, 2015), the participant loses the feeling of control over the movement just performed (Galvan Debarba et al., 2018; Kannape & Blanke, 2013), which is characterized by changes in the activation in premotor cortex (PMC; i.e., Seghezzi, Zirone, et al., 2019; Zito et al., 2020). The induction of bodily illusions while recording EEG or functional magnetic resonance imaging (fMRI) data enabled the discovery of a set of multisensory brain regions involved in the BSC process like the temporoparietal junction (which includes the angular gyrus), intraparietal sulcus, PMC and insula (Cabanis et al., 2013; Park & Blanke, 2019; Seghezzi, Giannini, et al., 2019). Critically, some of these regions, such as the angular gyrus and the precuneus, are often reported in studies investigating EM and ANC (Fletcher et al., 1995; Linden et al., 2017). Hence, the link between BSC and ANC is also supported by shared neural substrate.

1.5 Episodic memory and bodily self-consciousness

One of the first studies testing the influence of bodily context on EM was performed in 1967 (Rand & Wapner, 1967), showing that congruent body posture between encoding and retrieval facilitated memory retrieval of a list of words, thus highlighting the role of the body as a contextual cue facilitating memory retrieval. This finding was further extended to autobiographical memory forty years later by Dijkstra and colleagues (Dijkstra et al., 2007), who demonstrated that bodily context is relevant for EM encoded in everyday life and facilitates the retrieval of information years after encoding.

There are also important links between BSC and EM. 1PP, an essential component of BSC, has been related to EM. Based on original findings of Nigro & Neisser (1983), St-Jacques and colleagues demonstrated that the retrieval of memories in 3PP led to poorer recollection of the subjective and sensory information experienced at encoding (Iriye & Jacques, 2018; Iriye & St. Jacques, 2021; Schacter et al., 2011; St. Jacques, 2019; St. Jacques et al., 2017). These findings were reproduced by other researchers and linked at the neural level with activation of the precuneus whose activity and grey matter volume were positively correlated with the perspective adopted during the retrieval of the EM (Freton et al., 2014; Lundstrom et al., 2005; Trimble & Cavanna, 2008). Although these studies did not directly link EM with BSC, they are of fundamental importance because they present a first line of evidence that one of the main subcomponents of BSC, 1PP, impacts EM. However, most of these studies focused on the impact of a perspectival change at retrieval and thus did not provide information to explain how the subjective experience of the perspective *at encoding* affects EM.

To the best of my knowledge, the effect of perspective changes at encoding on EM has only been investigated in three studies. The first study showed that the encoding of an event in 3PP led to the decreased vividness of the memory and was linked with decreased activity in the left hippocampus during retrieval (Bergouignan et al., 2014). Two other studies showed a similar effect when an event was encoded in 1PP without seeing a body as compared to the

encoding of events from a naturalistic 1PP with a body view (Bréchet et al., 2019,2020; Gauthier et al., 2020). The effect of such BSC-related differences was related to the peri-encoding resting-state functional connectivity, showing increased connectivity between the right hippocampus and parahippocampus under naturalistic 1PP encoding (Gauthier et al., 2020). These three studies demonstrated that manipulation of the 1PP at encoding impacts EM retrieval. Nevertheless, it could be argued that those perspective-related changes are mainly due to a change of visual stimuli rather than a change of BSC state. Indeed, since the avatar observed from 3PP covers part of the visual field, one could argue that the 3PP lead to poorer EM due to the partially hidden visual field. However, a recent study brought additional evidence towards the effect of BSC on EM: emotional reliving and vividness of EM was shown to decrease when manipulating sense of ownership at encoding without change of perspective (Iriye & Ehrsson, 2022).

These studies provide first evidence about the impact of BSC at encoding on EM, but the results are mainly supported by behavioral evidence. Thus, the neural mechanisms supporting an association between BSC and EM remain unknown. Moreover, the few studies investigating the common neural substrate for BSC and EM mainly focused on the neural activity at retrieval. They did not investigate the neural mechanisms necessary to explain how a subjective experience linked to BSC at encoding impacts EM retrieval and how the brain mechanisms at encoding relate to those during retrieval. The present thesis aimed at bridging this gap by investigating how the brain activity at encoding is related to its activity at retrieval using functional magnetic resonance imaging (fMRI). Moreover, a new immersive VR and body tracking system was developed and fitted for usage inside the fMRI (Gauthier et al., 2021), enabling to induce controlled BSC manipulations during the encoding of virtual scenarios, hence making it possible to investigate the neural mechanisms linking BSC with EM.

1.6 Thesis outline and rationale

Throughout the five studies presented in this thesis, I used VR to induce sensory mismatches in healthy and clinical populations. The sensory mismatch altered BSC state and its related subjective experience (in the present thesis, SoA and sense of ownership). I measured EM when the BSC was preserved, that is, under visuomotor and perspectival congruency and compared it to when BSC was manipulated, thus altering its related subjective experience caused by the induction of the visuomotor and perspectival incongruency.

The first part of my thesis involved my main studies (Study 1 and Study 2) in which I[1] investigated how a BSC manipulation using visuomotor and perspectival mismatch influences the encoding process of EM (Study 1) and its related ANC at retrieval (Study 2). In the second part of my thesis, I investigated the role of BSC on EM in clinical populations. I applied the paradigm used in Studies 1 and 2 to the single case study of an amnestic patient with bilateral lesions in the hippocampus and deficits in EAM (Study 3). I also adapted the paradigm to test a small cohort of stroke patients (Study 4) to further explore the association between BSC and EM when brain regions related to BSC were lesioned. In the third part of my thesis, I collected the information related to VR features used in Studies 1-2 reported by the participants and discussed the role of VR features in the study of BSC (Study 5).

Study 1 includes a collection of four experiments where I investigated the effect of BSC manipulation during the encoding of virtual scenes and quantified the neural and behavioral changes induced by SoA modulation. Using an object recognition task, I designed a setup to test EM in immersive VR with motion tracking in fMRI. Results showed that hippocampus reinstatement was a neural proxy of memory, sensitive to BSC manipulation, and coupled with dorsal premotor cortex under visuomotor congruency only. Interestingly, opposite results were found in an amnestic patient with bilateral hippocampal lesions for whom preserved BSC led to decreased recognition performance compared to scenes encoded under strong visuomotor mismatch. These results put hippocampal reinstatement at the center of the association between BSC and EM, and provide meaningful evidence that the hippocampal-neocortical axis depend on the success of the sensorimotor integration and its related BSC state.

To better understand the specific association between SoA and the subjective aspect of EM retrieval, in Study 2, I investigated how the sensorimotor context at encoding affected ANC in participants from Study 1. I found that SoA was positively related to ANC only under visuomotor and perspectival congruency. This difference seemed to be mediated by the insula, whose functional connectivity at encoding with BSC and memory-related areas was positively related to ANC only under successful sensorimotor integration. Together, these

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[1] *Although the term « I » is used here, the present thesis is the result of a team work, see personal contributions*

results show that ANC depends on the sensorimotor aspect of BSC during the encoding of an event and that the insula mediates this process at the neural level.

Building on the sensitivity of hippocampal reinstatement to SoA manipulations found in healthy participants of Study 1, in Study 3, I did a follow-up study with the amnestic patient tested in Study 1 to better understand the impact of bodily cues on EM, potentially altered by her hippocampal lesions. Similarly to Study 1, I found that the patient had a better memory performance under visuomotor and perspectival mismatch, a condition associated with a strong BSC manipulation. This was further supported by an increased functional connectivity between the bilateral precuneus and medial prefrontal cortex and a decreased functional connectivity between both hippocampi and parahippocampi at rest compared to a cohort of age- and gender-matched controls. Together these results demonstrate that lesions in the hippocampus impair the retrieval of memories encoded under a preserved BSC.

In Study 4, I extended the investigation of BSC and EM in stroke patients with motor impairment at stroke onset. As the lesion provoked motor impairment, BSC is most likely impacted, therefore making it a suitable population to investigate the association between BSC and EM. I quantified patients' sensitivity to BSC manipulation using an adapted version of the experimental manipulation of Study 1 and Study 2. I found that patients with affected BSC sensitivity (no difference of SoA between visuomotor congruency and mismatch) had no difference of EM between conditions compared to patients with spared BSC sensitivity. Despite the small sample size, I discuss the unique value of testing stroke patients with motor impairments to investigate the association between the sensorimotor aspect of BSC and EM.

Finally, in Study 5, I reflected on the use of VR in the induction of bodily illusions and proposed improvements in virtual aesthetics to increase the strength of bodily illusions used in the study of BSC.

1.7 Personal contributions

My contributions to Studies 1-5 involved study design, data collection, data analysis, interpretation, and manuscript writing.

Study 1 *Bodily Self-Consciousness is associated with hippocampal and sensorimotor reinstatement of encoding activity*, **Nathalie Heidi Meyer***, Baptiste Gauthier* ,
Florian Lance, Juliette Boscheron, Mariana Babo Rebelo ,Sara Stampacchia, Michela Bassolino, Jevita Potheegadoo, Vincent Alvarez, Elizabeth Franc, Fabienne Esposito, Marilia Morais Lacerda, Bruno Herbelin, Olaf Blanke **in preparation**

Study 2 *Autonoetic consciousness depends on sense of agency and the sensorimotor context at encoding*, **Nathalie Heidi Meyer**, Baptiste Gauthier, Florian Lance,
Jevita Potheegadoo, Elizabeth Franc, Juliette Boscheron, Olaf Blanke **in preparation**

Study 3 *Altered association between bodily self-consciousness and episodic autobiographical memory in a rare case of amnesic patient,* **Nathalie Heidi Meyer***,
Mariana Babo Rebelo*, Jevita Potheegadoo, Bruno Herbelin, Sara Stampacchia, Fabienne Esposito, Marilia Morais Lacerda, Arthur Trivier, Florian Lance, Elena Beanato, Vincent Alvarez, Michela Bassolino, Olaf Blanke **in preparation**

Study 4 *Investigating sensorimotor alteration of bodily self-consciousness and its impact on episodic memory in stroke population: A proof of concept study*, **Nathalie Heidi Meyer**,
Baptiste Gauthier, Martino Ceroni, Lisa Fleury, Julia Brügger, Andeol Cadic Melchior,
Florian Lance, Jevita Potheegadoo, Sara Stampacchia, Friedhelm Hummel, Olaf Blanke **in preparation** *(Data collection)*

Study 5 *Bodily illusions in virtual reality: new insights into how VR features influence embodiment,* **Nathalie Heidi Meyer***, Sophie Betka*, Baptiste Gauthier, Elizabeth Franc, Juliette Boscheron, Bruno Herbelin, Florian Lance, Olaf Blanke **in preparation**

2. Study 1: Bodily Self-Consciousness is associated with hippocampal and sensorimotor reinstatement of encoding activity

Authors

Nathalie Heidi Meyer* [1], Baptiste Gauthier* [1,2], Florian Lance[1], Juliette Boscheron[1], Mariana Babo Rebelo[1], Sara Stampacchia[1], Michela Bassolino[3], Jevita Potheegadoo[1,] Vincent Alvarez[4], Elizabeth Franc[1], Fabienne Esposito[5], Marilia Morais Lacerda[5], Bruno Herbelin[1], Olaf Blanke [1, 6]

Affiliations

[1] Laboratory of Cognitive Neuroscience, Neuro-X Institute & Brain Mind Institute and Center for Neuroprosthetics, Faculty of Life Sciences, Ecole Polytechnique Fédérale de Lausanne, Geneva, Switzerland

[2] Clinical Research Unit, Neuchâtel Hospital Network, 2000 Neuchâtel, Switzerland

[3] School of Health Sciences, Haute École spécialisée de Suisse occidentale (HES-SO) Valais-Wallis, Sion, Switzerland.

[4] Hopital du Valais, Avenue Grand Champsec 80, 1950 Sion, Switzerland

[5] Clinique Romande de Réadaptation, SUVA,Avenue Grand Champsec 90, 1950 Sion, Switzerland

[6] Department of Clinical Neurosciences, University Hospital Geneva, Rue Micheli-du-Crest 24, 1205, Geneva Switzerland

*equal contributions

2.1 Abstract

Episodic memory (EM) depends on various parameters, such as emotional arousal, perceptual details, and sensory information at encoding and retrieval. Numerous studies have investigated the role of the sensory context, mostly visual and auditory, on EM retrieval. Although the body is a rich substrate providing various sensory stimuli such as tactile, proprioceptive, and vestibular, the role of the body context on EM formation and retrieval remains unknown. However, in addition to potentially providing important cues during EM retrieval, the body also contributes to the formation of a lower-level form of self-consciousness, called bodily self-consciousness (BSC), built on the integration of exteroceptive and interoceptive bodily signals. Although BSC might play a key role in linking EM, sensory context, and self-consciousness within a common framework, little is known about how it contributes to EM formation and retrieval.

Here we used immersive virtual reality (VR) to alter key aspects of the bodily self by manipulating visuomotor and perspectival congruency of the participants' bodies while encoding virtual scenes and recording brain activity during the encoding and retrieval of delayed scene recognition task. We found that manipulation of visuomotor and perspectival congruency altered the hippocampal reinstatement at retrieval and predicted EM performance. In addition, we found that hippocampal reinstatement was coupled with a network of cortical regions sensitive to the visuomotor and perspectival congruency consisting of the left dorsal premotor cortex (dPMC) and supplementary motor area (SMA). Moreover, the coupling of the hippocampal reinstatement with dPMC was specific to the visuomotor and perspectival congruency. Collectively, these results link the bodily context and its related subjective experience to reinstatement, a neural mechanism known to be involved in EM retrieval, with a reinstatement coupling between hippocampus and BSC-sensitive cortical regions.

2.2 Introduction

Episodic memory (EM) is a form of long-term declarative memory associated with the recall of the sensory details of an event in its unique spatiotemporal context (Tulving, 1985, 1972). EM retrieval is tightly linked to its encoding context and is modulated by various parameters such as emotional and perceptual context, and the sensory modalities during encoding, such as visual, auditory, or olfactory cues (Boccia et al., 2019; Dinh et al., 1999; Kensinger & Ford, 2020; Wheeler, 2000). A key neural mechanism of EM is reinstatement, that is, the reactivation of brain regions during the retrieval process that were activated during encoding (Mack & Preston, 2016; Oedekoven et al., 2017; Staresina et al., 2012; Xiao et al., 2017). Reinstatement was first observed in cortical areas. For example, some studies reported the activation of primary and extrastriate visual cortex during the retrieval of events containing visual stimuli as well as the reactivation of auditory brain regions during retrieval of EM containing auditory stimuli (Bosch et al., 2014; Wheeler, 2000). Moreover, reinstatement was also observed in the medial temporal lobe (in the hippocampus, parahippocampus, and perirhinal cortex ; Liang and Preston, 2017; Pacheco Estefan et al., 2019; Staresina et al., 2013; Tompary et al., 2016). More specifically, hippocampal reinstatement was associated with memory performance: higher hippocampal reinstatement for correct compared to incorrect item retrieval was demonstrated (Tompary et al., 2016), showing that hippocampal activity at retrieval was more similar to its activity at encoding when participants successfully retrieved items. Although reinstatement has been observed in both sensory cortical regions and medial temporal lobe regions, these data are compatible with the multiple trace theory (MTT). MTT proposes that the hippocampus is necessary for EM recollection and mediates the retrieval of sensory information stored in respective sensory cortical regions (Moscovitch et al., 2016; Nadel et al., 2000; Sekeres et al., 2017). This was further supported by evidence that hippocampal activity at encoding (Danker et al., 2017; E. A. Wing et al., 2015) and retrieval (Gordon et al., 2014; Ritchey et al., 2013; Staresina et al., 2012; Tompary et al., 2016) predicted the reinstatement of cortical areas at retrieval.

Concerning the sensory context of EM, most research has focused on how auditory and visual stimuli and their related brain activity were reinstated during the retrieval of EM (Bosch et al., 2014; Wheeler, 2000). However, the role of the observer's body in this context and the related sensory inputs such as tactile, proprioceptive, or vestibular and their integration with motor signals have only received scant interest. This neglect is surprising because the body provides a rich sensory-motor input during encoding and may provide cues that aid memory formation for visual and auditory stimuli. Although it was shown that congruent body posture between encoding and retrieval facilitated episodic memory retrieval of a word list (Rand & Wapner, 1967) and personal events (Dijkstra et al., 2007), the sensory body context has never been manipulated during encoding, and its relevance for EM and the involved brain mechanisms remain unknown.

Interestingly, bodily signals are also critical signals for an embodied or bodily form of self-consciousness, termed bodily self-consciousness (BSC; (Blanke & Metzinger, 2009; Ehrsson, 2012; Park & Blanke, 2019; Tsakiris et al., 2010). BSC is based on the integration of exteroceptive and interoceptive multisensory inputs (Aspell et al., 2009; Botvinick & Cohen, 1998; De Vignemont, 2011; Ionta et al., 2011; Jeannerod, 2007; Lenggenhager et al., 2007, 2009) and includes components such as the sense of agency (SoA, the feeling of being in control of one's own body), body ownership (the feeling tha the body belongs to oneself), the first-person perspective (1PP; the observation of the world from a body-centered perspective), and self-location (the feeling that the self is centered around a person's body; (Blanke & Metzinger, 2009; Park & Blanke, 2019). Alteration of specific components of BSC, such as self-location and 1PP can be performed experimentally using virtual reality (VR) and exposing participants to conflicting multisensory visuotactile or visuomotor stimulation (Blanke et al., 2015; Tsakiris, 2010) from either a first-person (Ehrsson, 2007; Lenggenhager et al., 2007) or a third-person perspective (3PP;(Ionta et al., 2011; Lenggenhager et al., 2007; Pfeiffer et al., 2016). Visuomotor and perspectival incongruencies have also been shown to modulate the SoA (Fourneret & Jeannerod, 1998; Frank et al., 2001; Kannape et al., 2010; Kannape & Blanke, 2013; Salomon et al., 2022). At the neural level, BSC is mediated by a frontoparietal network consisting of premotor cortex, posterior parietal cortex, and posterior regions of the superior temporal sulcus (Blanke, 2012; Grivaz et al., 2017; Ionta et al., 2011; V. Petkova et al., 2011), however, not much is known whether and how experimentally-induced changes in BSC impact the neural processes of encoding and retrieval of EM.

Recent evidence demonstrated that conflicting multisensory and sensorimotor stimulation influences spatial and episodic memory (Iriye & Jacques, 2018; Iriye & St. Jacques, 2021; Moon et al., 2022; Nigro & Neisser, 1983; Schacter et al., 2011; St. Jacques, 2019). For example, the work of St. Jacques and colleagues showed that the retrieval of an event from a 3PP led to poorer recollection of the sensory and perceptual details experienced at encoding, characterized at the neural level by changes of activity in the posterior parietal regions (Iriye & Jacques, 2018; Iriye & St. Jacques, 2021; Schacter et al., 2011; St. Jacques, 2019; St. Jacques et al., 2017). Other recent studies focused on the role of the body context and BSC on EM. Thus, exposing participants to sensorimotor conflicts decreased spatial memory performance and related specific activity in entorhinal cortex (Moon et al., 2022). Moreover, items seen from a natural 1PP were associated with more vivid memories and better memory performance compared to an event encoded from the 3PP or with no body view (Bergouignan et al., 2014; Bréchet et al., 2019, 2020; Gauthier et al., 2020; Iriye & Ehrsson, 2022). More recently, it was further shown that a reduced sense of body ownership decreased EM (Iriye & Ehrsson, 2022). Collectively, these studies suggest that an alteration of BSC in the present, that is during the encoding of an event, affects self-related memory past events.

Critically, most of these studies investigated the effects of BSC modulation on EM behavior (Bergouignan et al., 2014; Bréchet et al., 2019, 2020; Gauthier et al., 2020; Iriye & Ehrsson, 2022), whereas only two studies investigated the neural substrate with a specific focus in the

hippocampus (Bergouignan et al., 2014; Bréchet et al., 2019, 2020; Gauthier et al., 2020; Iriye & Ehrsson, 2022). Thus, hippocampal activity during the retrieval of an event has been related to the vividness of the recollection, depending on the perspective (1PP and 3PP) adopted at encoding (Bergouignan et al., 2014). Another study described functional connectivity changes between the right hippocampus and the right parahippocampus, depending on whether participants, during encoding, saw their body from their habitual 1PP or not (Gauthier et al., 2020). Although both of these studies support the role of BSC in EM processes, because they did not record the brain activity during both encoding and retrieval, they do not provide insight into the neural mechanism involved in the change of hippocampal activity and connectivity. Thus, they could not test whether reinstatement mechanism is sensitive to BSC manipulation. Additionally, they did not link (and sometimes even did not measure) the subjective experience related to BSC. Therefore, they could not investigate how a bodily-subjective experience at encoding impacted EM retrieval and its neural activity.

In the present study, we aimed to bridge this gap by investigating how BSC impacts EM during the encoding of virtual scenes in a series of four experiments with a total of 76 healthy subjects and a rare amnesic patient with bilateral hippocampal damage. We designed a task to test episodic memory one hour after an encoding session, inspired by previous lab work (Gauthier et al., 2020, Bréchet et al., 2020, Bréchet et al., 2019). In Experiment 1, we tested participants behaviorally under incidental encoding in a replicate of an MR scanner. We then replicated the same experiment in an MR scanner to simultaneously record the functional brain activity during both encoding and recognition session in Experiment 2. In Experiment 3, we performed the same experiments behaviorally on healthy participants under intentional encoding instruction to better understand the effect of BSC on EM when participants were not naïve to the task. In Experiment 4, we tested an amnesic patient with bilateral damage in the hippocampus with the same paradigm than Experiment 1 to 3 to better understand how the association between BSC and EM was modulated by the patient's lesions. In each Experiment, we investigated the effect of a change of BSC on recognition performance and expected to have better recognition performance under non-manipulated BSC. We combined fully immersive VR with motion tracking and fMRI to alter BSC using different levels of visuomotor and perspectival congruency during the incidental encoding of objects presented in three virtual scenes. Each scene was associated with a specific experimental condition differing in visuomotor and perspectival congruency (first-person synchronous avatar, first-person asynchronous avatar, and third-person asynchronous avatar). BSC was assessed in a separate session in a fourth immersive virtual scene, and EM was tested one hour later using a scene recognition task, reimmersing our participants in the same virtual scenes but without the avatar and the related BSC manipulation. We expected to find higher SoA and better memory performance for the scene encoded under visuomotor and perspectival congruency. At the neuroimaging level, we expected to find higher reinstatement during successful trials in the recognition task for scene encoded under visuomotor and perspectival congruency. Our results show that hippocampal reinstatement was sensitive to BSC manipulation and linked with memory performance.

2.3 Results

We immersed participants in VR and tested memory for complex indoor scenes in three experimental conditions, differing in levels of BSC, as manipulated by visuomotor and perspectival congruency. In each condition, participants were immersed and observed an avatar while moving their right hand. In the first condition, the avatar was observed from a 1PP, and moved synchronously with participants' upper limb movement (SYNCH1PP; visuomotor and perspectival congruency, no manipulation of BSC). In the second condition, the avatar was observed from a 1PP but the avatar movement was delayed with respect to the participants' upper limb movement (ASYNCH1PP; visuomotor mismatch, altered BSC). Finally, in the third condition, participants observed an avatar from a 3PP and the movement was delayed as well (ASYNCH3PP; visuomotor and perspectival mismatch, strong alteration of BSC). Memory for the scenes was tested one hour after the encoding session in a recognition task where participants were immersed in three different virtual scenes (**Figure 1**; randomized across participants). Critically, during the recognition task, no avatar or body view was implemented, thus, all scenes were observed from the same location as during encoding, but without any avatar and without manipulation of visuomotor and perspectival congruency. The VR scene was either a scene (**Figure 1**) containing the same objects (as shown during the encoding session) or a scene that contained the same number of objects, of which one was changed compared to the encoding session. Healthy participants were asked to report if the scene had changed compared to the encoding session or not. SoA and other aspects of BSC and their modulation across the three conditions were assessed using a different complex outdoor scene, to avoid any interference with the encoding of the three scenes used during encoding and recognition sessions (**Figure 1**). Encoding was incidental in Experiments 1 and 2, that is, participants were not told during encoding that their memory was later tested for the scenes (see methods). In Experiment 1, the task was only behavioral, and in Experiment 2, we recorded the brain activity of participants during the Encoding, BSC assessment and recognition session. In Experiment 3 we tested participants behaviorially under intentional instruction, in order to better understand whether the effect of BSC on EM would be dependent on the type of encoding (incidental versus intentional). Since Experiments 1 and 2 were performed under similar instructions, we combined both samples for behavioral analysis. Because our primary interest was to understand how the SoA, as manipulated by visuomotor and perspectival congruency, modulates EM, we compared the synchronous condition seen from the congruent first-person viewpoint (visuomotor and perspectival congruency; SYNCH1PP) with the two conditions in which visuomotor and perspectival congruency was altered (ASYNCH1PP, ASYNCH3PP). In the following section, we first describe the behavioral results of Experiment 1 to 3 and then focus on the imaging results of Experiment 2.
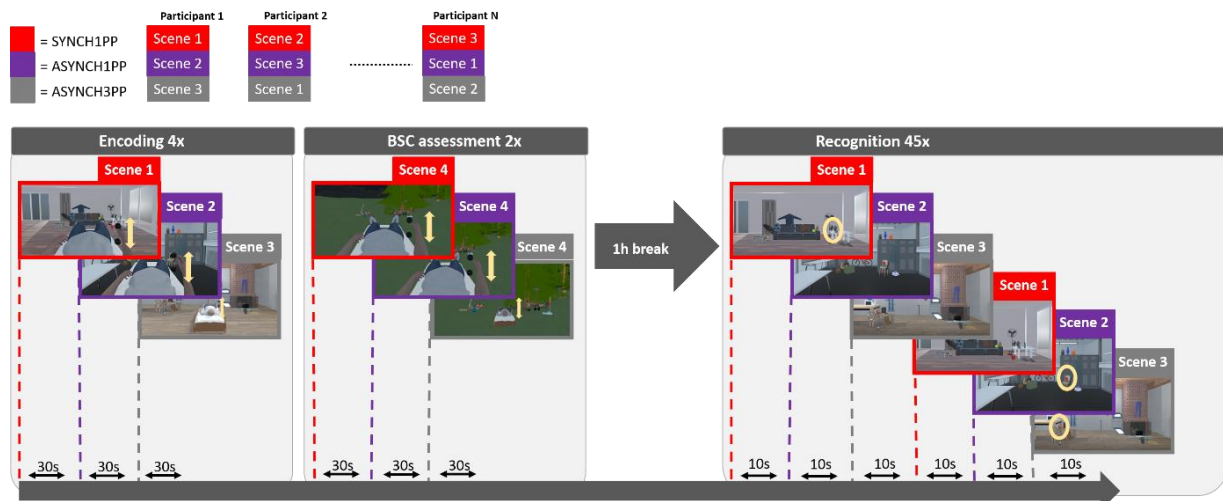
Figure 1: Experimental design. *The encoding of 3 immersive virtual scenes was associated with three levels of bodily self-consciousness (BSC) combining avatar perspective (first person avatar = 1PP or third person avatar = 3PP) and avatar movement synchrony (SYNCH or ASYNCH) in 3 levels of BSC alterations: SYNCH1PP (unaltered), ASYNCH1PP (altered) and ASYNCH3PP (strongly altered). One hour after the encoding session, the memory of the scenes was assessed with a recognition task. The recognition task was performed with no avatar, thus, the conditions were attributed solely based on encoding association. The subjective experience of BSC alterations was tested for each condition in an independent session within a fourth scene to avoid memory interference. The association between scene and conditions was pseudorandomized between participants. During encoding (leftmost panel), participants performed a vertical movement with their right arm between two visual landmarks. The BSC assessment (middle panel) was identical to encoding but in a different unique scene. The recognition task (rightmost panel) consisted in detecting changes in scenes that were either perfectly identical to encoded scenes or with a single object change. This design was used for the four experiments reported in this study.*

Higher SoA during incidental encoding when immersed with visuomotor and perspectival congruency (behavior, Experiment 1 and 2)

To quantify the difference in SoA under the different conditions we applied a linear mixed model for each of the questions asked during the BSC assessment. As predicted, SoA was higher in SYNCH1PP as compared to both other conditions with visuomotor and perspectival mismatch (ASYNCH1PP: estimate = -0.07, t = -2.93, p = 0.003; ASYNCH3PP: estimate = -0.07, t = -2.84, p = 0.005; **Figure 2A**). Ratings were much lower and close to zero for the control questions (**Figure 2A**; SYNCH1PP compared to ASYNCH1PP: estimate = 0.01, t = 0.94, p = 0.35; SYNCH1PP compared to ASYNCH3PP: estimate = -0.01, t = -1.04, p = 0.3) and differed from the SoA ratings (estimate = -0.47, t = -26.17, p <0.0001). Applying the same approach to the items about body ownership and threat, we found that participants rated their body ownership significantly higher in SYNCH1PP than ASYNCH3PP (estimate = -0.09, t = -2.9, p = 0.004). Threat was also rated as stronger in SYNCH1PP compared to ASYNCH3PP (estimate = -0.18, t = -4.45, p <0.0001). The ratings were not significantly different when comparing SYNCH1PP with ASYNCH1PP (body ownership: estimate = 0.01, t = 0.39, p = 0.7; Threat: estimate = - 0.037, t= -0.94, p = 0.35; **Supplementary Figure 1A**). There was no difference between Experiment 1 and 2 when adding Experiment as a variable in the model (see Supplementary table 1-4 for the details of the model).
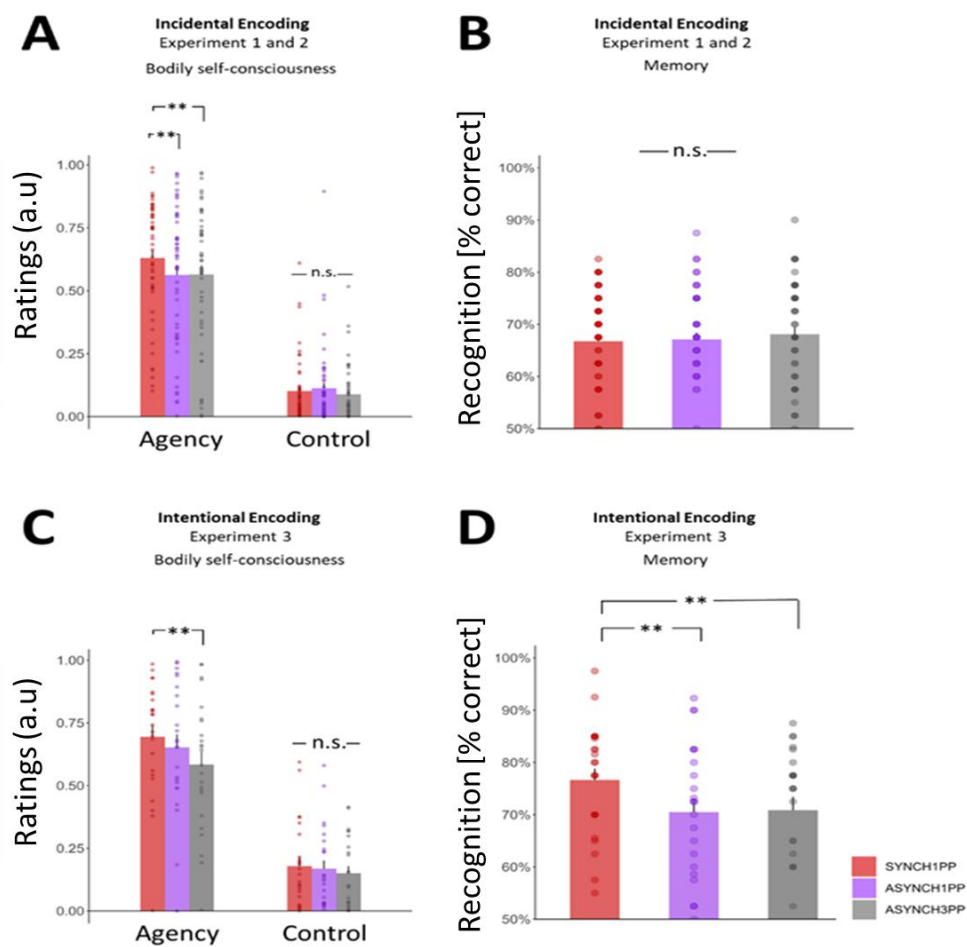
*Figure 2: Higher sense of agency (SoA) under visuomotor and perspectival congruency is associated with higher memory performance under intentional encoding. A. SoA under incidental encoding instruction. Participants had a higher SoA in SYNCH1PP compared to the two other conditions. ** indicates significance level with p-value <0.01 as tested with a linear mixed model using SoA as dependent variable and conditions as fixed factor. SoA was computed as the average rating of participants in the BSC assessment for the SoA question. N = 50 young healthy participants. B. Recognition performance under incidental encoding instruction. There was no difference in recognition performance between conditions (as tested with mixed effect logistic regression with recognition performance (binary) as dependent variable and conditions and scene as fixed factor; N = 48 young healthy participants. C. SoA under intentional encoding instruction. Participants felt significantly more agent of their movement in SYNCH1PP compared to ASYNCH3PP, no difference was observed between SYNCH1PP and ASYNCH1PP. ** indicates significance level with p-value <0.01 as tested with a linear mixed model using SoA as dependent variable and conditions as fixed factor ; N = 25 young healthy participants D. Recognition performance under intentional encoding instruction. Participants had a better recognition performance in SYNCH1PP compared to the other conditions. ** indicates significance level with p-value <0.01 as tested with mixed effect logistic regression with recognition performance (binary) as dependent variable and conditions and scene as fixed factor; N = 24 young healthy participants. A.u = arbitrary unit.*

Visuomotor and perspectival congruency during incidental encoding and object recognition (behavior, Experiment 1 and 2)

To investigate the effect of visuomotor and perspectival congruency during encoding on recognition performance, we tested participants with a recognition task one hour after the encoding session. Critically, although participants were immersed in the same virtual scenes

during the recognition task, they did not see an avatar and there was no manipulation of visuomotor or perspectival congruency during the recognition task. During incidental encoding, participants showed no significant difference in recognition performance (accuracy) between the three experimental conditions (**Figure 2B**, SYNCH1PP vs. ASYNCH1PP estimate = 0.03, z = 0.4, p = 0.73; SYNCH1PP vs. ASYNCH3PP estimate = 0.06, z = 0.93, p = 0.35). There was no difference in recognition performance between both Experiment 1 and 2 (estimate = -0.02, z = -0.24, p = 0.8, see Supplementary table 5).

Intentional encoding. Higher SoA and better recognition performance for intentional encoding when immersed with visuomotor and perspectival congruency (behavior, Experiment 3)

Experiment 3 was similar in all aspects, except that participants were told before the encoding session that their memory was later tested for the scenes (intentional encoding). As in Experiments 1 and 2, participants' SoA was higher in SYNCH1PP compared to ASYNCH3PP (**Figure 2C**; estimate = -0.11, t = -3.16, p = 0.002; the comparison between the SYNCH1PP and the ASYNCH1PP condition was not significant, but similar compared to Experiment 1 and 2 (estimate = -0.04, t = -1.2, p = 0.23). The average control ratings were significantly lower than SoA ratings (estimate = -0.47, t = -17.6, p <0.0001) and not significantly different between conditions (SYNCH1PP compared to ASYNCH1PP: estimate = -0.01, t = -0.56, p = 0.58; SYNCH1PP compared to ASYNCH3PP: estimate = -0.028, t = -1.5, p = 0.13). Experiments 1 and 2 also showed higher body ownership and threat ratings in SYNCH1PP versus ASYNCH3PP (body ownership: estimate = -0.2, t= -4.6, p <0.0001; threat: estimate = -0.22, t = -3.13, p = 0.002; **Supplementary Figure 1B**). There was no significant difference in body ownership and threat ratings when SYNCH1PP was compared with ASYNCH1PP (body ownership: estimate = -0.06, t = -1.23, p = 0.22; threat: estimate = -0.04, t = -0.5, p = 0.61, Supplementary table 7-10).

For the one-hour delayed recognition task, we found that participants had significantly higher performance in the SYNCH1PP condition compared to ASYNCH1PP (**Figure 2D**, estimate = -0.33, z = -3.06, p = 0.002) and to ASYNCH3PP (estimate = -0.32, z = -2.95, p = 0.003, Supplementary table 11). To summarize, these behavioral results from three experiments demonstrate that the SYNCH1PP condition induces a higher SoA by exposing participants to objects that were embedded in a 3D VR scene and seen under visuomotor and perspectival congruency during intentional and incidental encoding. Concerning memory, one-hour delayed recognition was boosted for scenes encoded in the SYNCH1PP condition for intentional but not incidental encoding.

Lateralized recognition performance visuomotor and perspectival congruency (behavior, Experiments 1-3)

We next investigated whether the laterality of objects (right versus left) that were tested impacted recognition performance, because participants moved their right arm during encoding. Such right-handed movements that were shown in the immersive scenes during the encoding sessions could have decreased recognition performance due to visual occlusion of the objects placed on the right side or may have, on the contrary, improved recognition performance due to motor facilitation (right-sided arm movements), enhanced attention towards the right side. Results for Experiments 1 and 2 showed that participants had better recognition performance for right-sided objects, irrespective of condition (**Supplementary Figure 2A**; Supplementary table 6; estimate = 0.288, z = 2.028, p = 0.043). Applying the same analysis to data from Experiment 3 (i.e., right- versus left-sided objects), we found no effect of object laterality (estimate = 0.037, z= 0.168, p = 0.867 **Supplementary Figure 2B**) and no interaction with condition (Supplementary table 12), showing that attention or movement-related processes did not differently impact recognition performance in Experiment 3. These data suggest that processes related to attention and/or hand movements may enhance recognition performance for right-sided versus left-sided objects, but only during incidental encoding. Critically, this did not differ between our three experimental conditions in either of the three experiments.

fMRI (Experiment 2)

Experiment 2 (fMRI, 29 participants) was identical to Experiment 1 (mock scanner, 26 participants), and we recorded fMRI during the three critical periods of the experiment: during the encoding session, during the BSC assessment session, and during the 1-hour delayed recognition session. During all three sessions, participants were exposed to different immersive VR conditions (see **Figure 1**). We carried out the following fMRI analyses. First, we carried out a searchlight representational similarity analysis (RSA) to identify brain areas that were modulated by visuomotor and perspectival congruency and, critically, similarly modulated during both encoding and recognition. Thus, RSA searched for the reinstatement of encoding activity during the recognition task that was modulated by our experimental manipulation of visuomotor and perspectival congruency. Because RSA did not allow us to quantify the *level of similarity* for each condition separately, we computed the encoding-recognition similarity scores (ERS) for each condition and participant and each of the brain regions identified with the RSA. Finally, we investigated if ERS for regions showing significant ERS scores difference was associated with participants' recognition performance.

RSA analysis. Level of visuomotor and perspectival congruency impacts the reinstatement of encoding activity during recognition

We first explored the condition-dependent reinstatement of encoding activity across the whole brain. To identify reinstatement of brain activity during the encoding and the recognition session, which was similarly modulated by visuomotor and perspectival congruency, we applied a searchlight RSA procedure (**Figure 3A**). RSA analysis revealed four regions (**Figure 3B**): left hippocampus, left middle temporal gyrus (MTG), visual cortex, and orbitofrontal cortex (Npermutation = 1000, p <0.05, cluster size> 500 voxels). The left hippocampus (MNI coordinates -26, -22, -15) is often reported in memory research (i.e., Burgess et al., 2002; Daselaar et al., 2008; Tulving and Markowitsch, 1998) and the middle temporal gyrus (MNI coordinates -59, -33, -3) has been involved in item recognition (Yonelinas et al., 2001). RSA also identified visual cortex (MNI coordinate -18,-55,-2) that has been reported in memory for visual stimuli (Yamamoto et al., 2005) and left orbitofrontal cortex (MNI coordinate -30,56,-1) involved in EM consolidation (Rolls, 2022). To summarize, RSA identified brain activity in four regions that showed similar differences during encoding and recognition and depended on level of visuomotor and perspectival congruency.
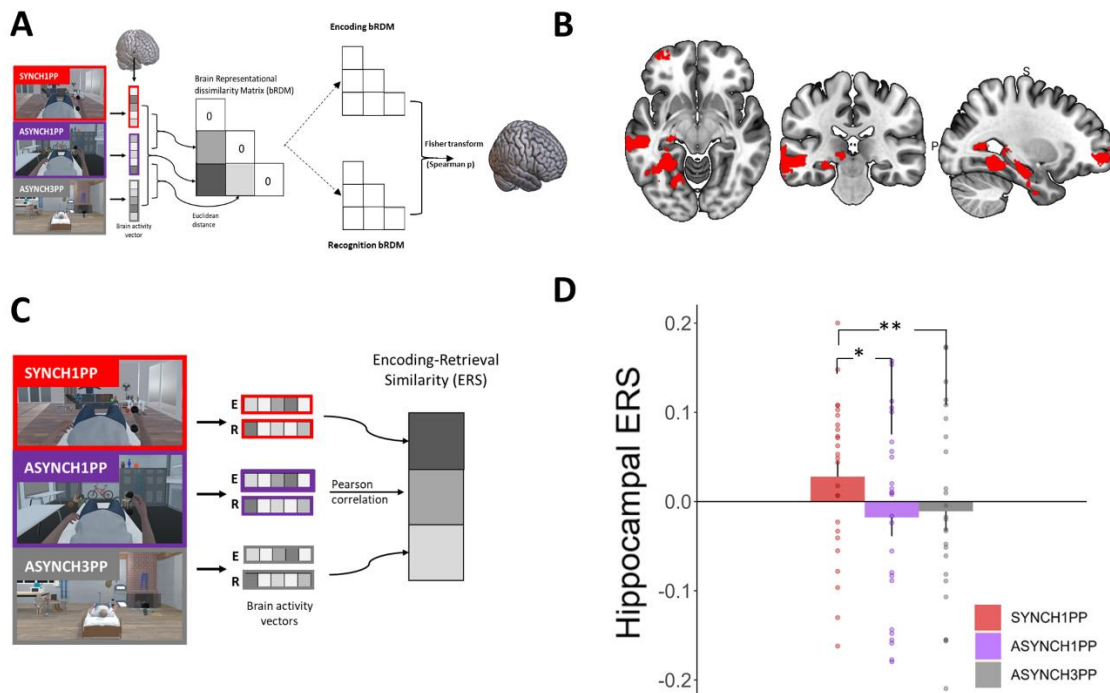
*Figure 3: Left hippocampal encoding-recognition similarity (ERS) is higher under visuomotor and perspectival congruency and correlates with recognition. A. Searchlight encoding-recognition representational similarity (RSA). We applied an RSA to identify brain regions that had same pattern of difference between conditions during encoding and recognition sessions in Experiment 2 (N = 25 young healthy participants). B. Encoding-recognition RSA maps. We found four regions, the left hippocampus, bilateral calcarine cortex, the left middle temporal and left frontal superior orbital gyrus, which survived permutation test (N_{permutation} = 1000, p <0.05, cluster size> 500). C. ERS. We computed the ERS of the regions identified by the RSA applying a Pearson correlation between the voxel activity at encoding and their activity at recognition for each of the brain region in Experiment 2 (N = 25 young healthy participants). D. Hippocampal ERS is higher under visuomotor and perspectival congruency. Hippocampal ERS averaged on success was significantly higher under visuomotor and perspectival congruency (SYNCH1PP) compared to the two other conditions. *, ** indicates significance level with p-value <0.05 and <0.01 respectively as tested with a linear mixed model with hippocampal ERS as dependent variable and conditions as factor. ERS = Encoding recognition similarity score.*

ERS analysis. Reinstatement of encoding activity in the left hippocampus is higher for visuomotor and perspectival congruency and indexes recognition memory.

Although RSA analysis identified four regions that showed a similar pattern of activity between encoding and recognition, it does not provide information about the similarity *per conditions* of activity between encoding and recognition. To further quantify the similarity of activity of these four brain regions between encoding and recognition, we computed their ERS for each of the three conditions (Danker et al., 2017; Ritchey et al., 2012; Wing et al., 2013; **Figure 3C**). This analysis revealed that ERS in the left hippocampus was significantly higher in SYNCH1PP compared to the two conditions with visuomotor and perspectival incongruency (**Figure 3D**; SYNCH1PP vs. ASYNCH1PP estimate = -0.045, t = -2.57, p = 0.01; SYNCH1PP vs. ASYNCH3PP estimate = -0.045, t = -2.6, p = 0.009). There was also a higher ERS in SYNCH1PP compared to ASYNCH1PP in the left MTG (SYNCH1PP vs ASYNCH1PP estimate = -0.048, t = -2.77, p = 0.006). No such ERS differences were observed in visual cortex nor in orbitofrontal cortex (see Supplementary table 14-16 for detailed results). Based on previous studies showing that hippocampal ERS is a predictor of recognition memory (Ritchey et al., 2013; Tompary et al., 2016), we investigated whether the ERS of the left hippocampus and of the left MTG correlated with participants' recognition performance. Applying a linear mixed model (to explain recognition performance using hippocampal ERS; see Supplementary text for more details about model selection) revealed that ERS of the left hippocampus positively correlated with recognition performance, irrespective of condition (**Figure 4A**; estimate = 0.29, t = 2.72, p = 0.006, $<p_{corr}$ = 0.0125, Supplementary table 18, Supplementary text). We found a similar relationship between hippocampal ERS and performance in a trial-by-trial model but reaching significance only in the condition characterized by visuomotor and perspectival congruency (**Figure 4B**, Supplementary text). The same ERS analysis for the left MTG did not detect a significant association with recognition performance (See Supplementary table 20).
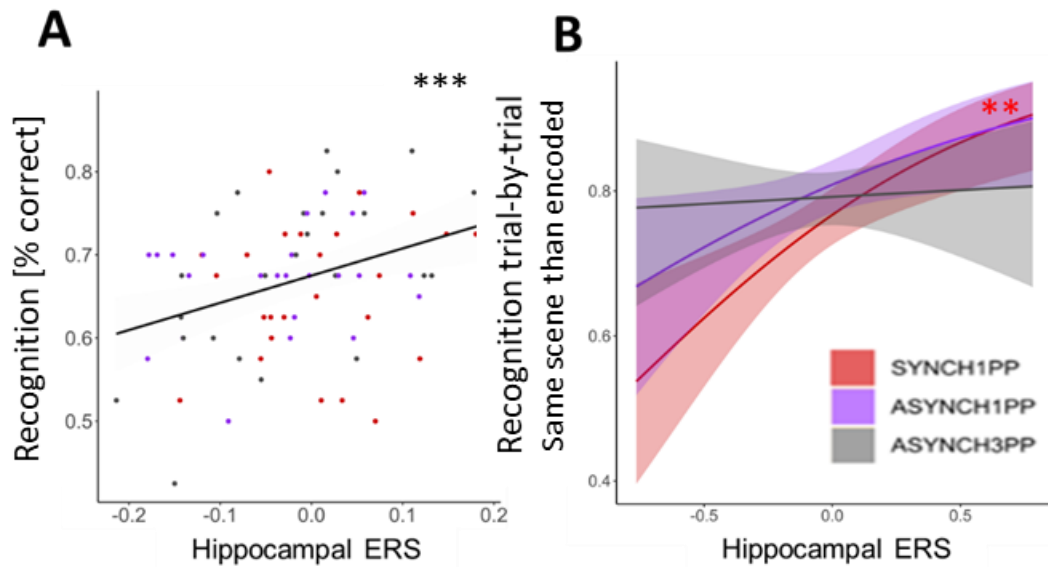
*Figure 4: Hippocampal reinstatement and performance. **A. Hippocampal ERS correlates with recognition**. Hippocampal ERS was significantly positively correlated with the recognition performance irrespective of conditions and survived multiple comparisons in Experiment 2 p = 0.008, $p_{corrected}$ = 0.013 as tested with a linear mixed model with the recognition performance (binary) as dependent variable (N = 25 young healthy participants). For better visualization the figure plot the recognition performance as percent correct answer for each condition (SYNCH1PP in red, ASYNCH1PP in purple and ASYNCH3PP in grey). **B. Trial-by-trial hippocampal ERS correlates with recognition of scene presented at encoding.** Recognition performance was explained by hippocampal ERS under visuomotor and perspectival congruency when the stimuli presented was the original scene. Hippocampal ERS in SYNCH1PP (red) positively predicted participants' recognition performance. *** indicates significance level with p-value <0.0001 as tested with mixed effect logistic regression. ERS = Encoding recognition similarity score.*

Hippocampal-neocortical interactions revealed by ERS are modulated by visuomotor and perspectival congruency

In a final step, we determined brain activity related to the SoA and then investigated whether it was associated with the condition-dependent reinstatement of encoding activity. To do so we first used univariate GLM and identified brain regions modulated by the visuomotor and perspectival congruency during the BSC session. Then we quantified the relation between ERS of these regions with the ERS of the left hippocampal activity.

First, we investigated which brain regions were sensitive to the SoA as manipulated during the BSC session. By contrasting SYNCH1PP with ASYNCH1PP and ASYNCH3PP (SYNCH1PP > ASYNCH1PP+ASYNCH3PP; second level within-subject ANOVA) during the BSC session, we identified a SoA network (**Figure 5A**) composed of left dorsal premotor cortex (dPMC, MNI coordinate -18, -24, 62) and bilateral supplementary motor area (SMA, MNI coordinate right SMA 4, -4, 55, left SMA -4, -11, 56, Supplementary table 19). Post-hoc analysis showed that the activity in these regions correlated with participant's SoA (Supplementary text). Second, we analyzed the interaction between these three brain regions (left dPMC and bilateral SMA) and the left hippocampus (as revealed by RSA and ERS analysis), by applying a linear mixed model investigating how the hippocampal ERS (reflecting recognition performance; dependent variable) was related to the ERS of the left dPMC and bilateral SMA (SoA sensitive regions), for each level of visuomotor and perspectival congruency. This analysis revealed a

significant difference in the coupling of the left hippocampal ERS and left dPMC ERS that depended on the experimental condition (**Figure 5B**; i.e., significant interaction between SYNCH1PP and ASYNCH1PP; ERS dPMC estimate = -0.19, t = -5.2, p <0.0001, Supplementary table 21). These data show that activity in a key memory region (hippocampus) differently correlates with activity in a key SoA region (dPMC), depending on visuomotor and perspectival congruency. This was further extended by post-hoc analysis, revealing that the dPMC ERS was significantly positively correlated with hippocampal ERS in SYNCH1PP (estimate = 0.18, t = 6.4, p <0.0001), but not significantly correlated with hippocampal ERS in the ASYNCH1PP condition (ASYNCH1PP: estimate = -0.04, t = -1.58, p = 0.12, Supplementary table 22-23). This shows that higher similarity between encoding and retrieval in the hippocampus (hippocampal ERS) is linked to a higher similarity between encoding and retrieval in an SoA sensitive region, dPMC, only in the condition with visuomotor and perspectival congruency, characterized by the highest SoA in the present experiments. Performing the same analysis for SMA and left hippocampus, hippocampal ERS was also associated with the left SMA (estimate = 0.07, t = 2.65, p = 0.008 Supplementary table 24). Such hippocampal-SMA coupling was characterized by a positive correlation but did not differ across conditions as found for hippocampal-dPMC coupling. The same analysis applied for the right SMA did not show any coupling with hippocampal ERS (Supplementary text and Supplementary table 25).
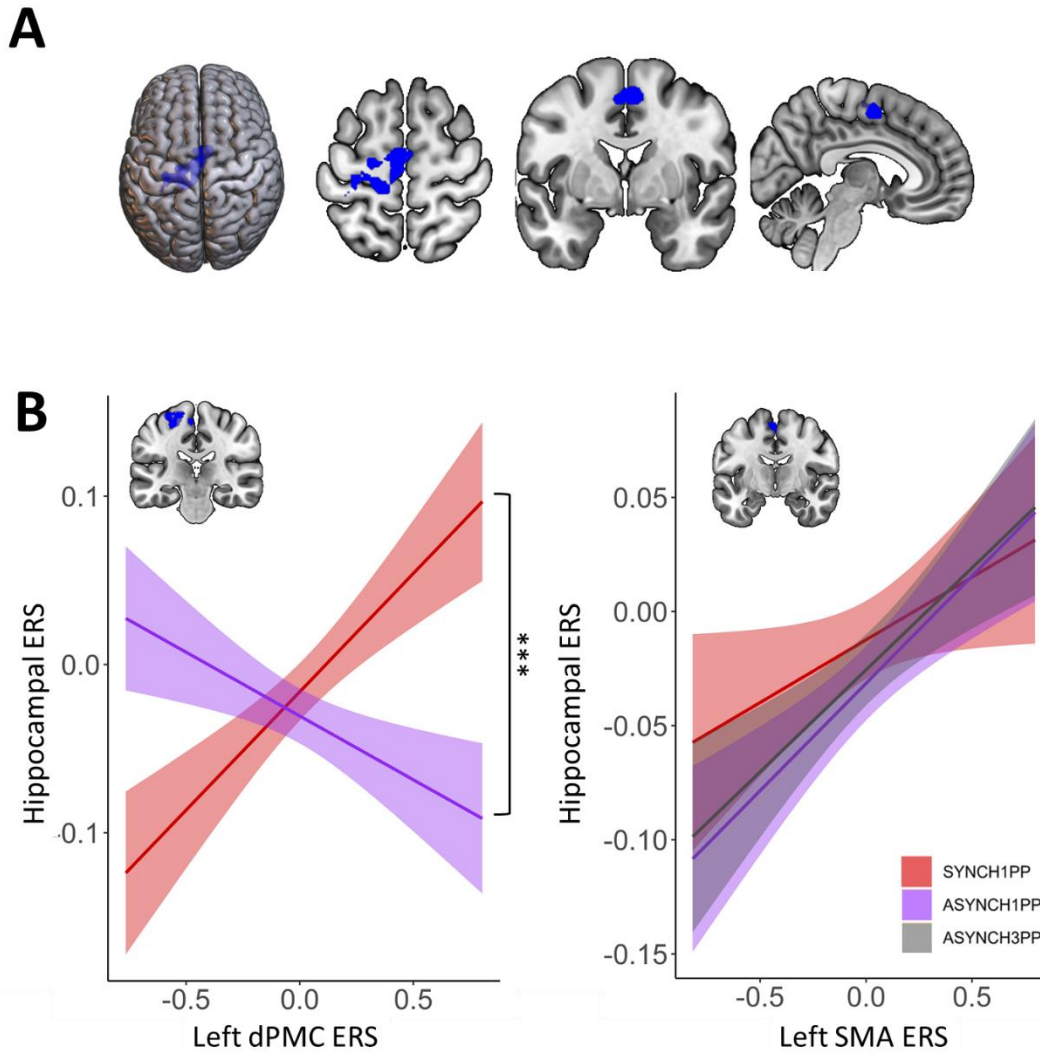
*Figure 5: Neural reinstatement in SoA regions correlates with left hippocampal reinstatement under visuomotor and perspectival congruency. A. univariate neural correlates of SoA. We found that the left dPMC and bilateral SMA (blue) at encoding were more activated under visuomotor and perspectival congruency (SYNCH1PP) compared to the two other conditions (N = 26 young healthy participants from Experiment 2). B. Hippocampal reinstatement is positively related to the reinstatement of SoA regions under visuomotor and perspectival congruency. ERS of the dPMC was found to correlate positively with hippocampal ERS under visuomotor and perspectival congruency (SYNCH1PP, red). *** indicates significance level with p-value <0.001 as tested with a linear mixed model with hippocampal ERS as dependent variable conditions as factor with an interaction with dPMC ERS. ERS of the left SMA was found to correlate positively with hippocampal ERS irrespective of condition p = 0.01 as tested with a linear mixed model with hippocampal ERS as dependent variable conditions as factor with an interaction with SMA ERS. N = 24 young healthy participants, dPMC = dorsal premotor cortex, SMA = Supplementary motor area, ERS = Encoding recognition similarity score.*

To summarize, we found that reinstatement-related activity in the left hippocampus, activity that we linked with performance in scene recognition, is systematically related to activity within a cortical SoA network consisting of left dPMC (contralateral to the moving right hand) and bilateral SMA. Whereas hippocampal-SMA coupling was present in all three conditions (reflecting a more general coupling), hippocampal-premotor coupling in the left hemisphere was found for reinstatement-related activity. It was stronger under visuomotor and perspectival congruency, suggesting a neural mechanism linking SoA and recognition of objects in complex three-dimensional scenes.

Amnestic patient with bilateral hippocampal damage is impaired in recognizing objects encoded with visuomotor and perspectival congruency

Would damage to the left hippocampus and its connections with PMC and SMA, impair the present SoA effects on recognition performance, mediated by visuomotor and perspectival congruency during encoding? We had the unique opportunity to investigate these behavioral and neural mechanisms in a patient suffering from a moderate to severe deficit in autobiographical and EM following a fungal brain infection. The patient showed severe retrograde amnesia (i.e., her daughter's wedding, holidays, and other important family events) and has participated in neuropsychological rehabilitation to relearn the "timeline" of her past. Despite relearning key facts about her life prior to the infection, the patient is to this day not able to re-experience these key events of her life. Her amnesia also extends to new memory following the fungal infection, for which she also has impaired recollection (moderate to severe anterograde amnesia).

Brain damage centered in the bilateral hippocampus and adjacent regions and included part of the parahippocampus and the amygdala (**Figure 6** and **Supplementary Figure 3**). Thus, the patient's hippocampal damage involved the left hippocampal region as detected by the present RSA and ERS analysis in study 2, performed in healthy participants. Five months after her hospitalization, we were able to test the patient and adapted the immersive VR paradigm tested in healthy participants to the patient. We tested her with the same scenes (as Experiment 1-3), in the same three conditions (SYNCH1PP, ASYNCH1PP, ASYNCH3PP), and with the same number of trials. She managed to perform all three sessions: the encoding session, the BSC session, and a one-hour delayed recognition session (see Methods for detail).
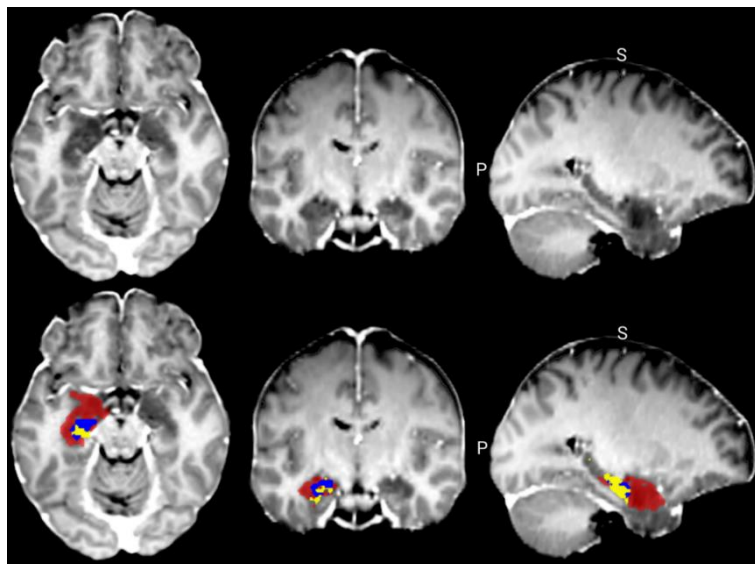
Figure 6: Amnestic patient with hippocampal damage. Structural scan of the patient's lesions (top panel) dating from the diagnosis day. Overlap of the patient's lesions and the left hippocampus identified with the representational similarity analysis (RSA, lower panel). Patient's lesions (red) and its overlap (blue) with the left hippocampus identified when applying an RSA analysis (yellow) between encoding and recognition session.

As predicted based on her MRI and her neuropsychological examination, results from the BSC session revealed that the patient had preserved SoA ratings comparable with those observed in healthy participants in Experiments 1-3. Thus, she had higher SoA ratings in the SYNCH1PP condition compared to both ASYNCH1PP and ASYNCH3PP conditions. The difference in the patient's SoA ratings between the SYNCH1PP condition and both other conditions (ASYNCH1PP and ASYNCH3PP) was modulated in the same way as observed in the healthy participants (**Figure 7A**) and her sensitivity to the manipulation was even higher compared to healthy participants, due to a larger difference between SoA ratings (SYNCH1PP compared to ASYNCH1PP (mean = 0.05, sd ± = 0.16, p < .001); ASYNCH1PP compared to ASYNCH3PP (mean = 0.03, sd ± = 0.16, p = 0.004). Similar findings were obtained for ownership ratings (higher ratings in the SYNCH1PP versus the two other conditions, compared to healthy participants; see Supplementary text). The patient's ratings for control items were low (**Figure 7B**), did not differ between conditions, and also did not differ from those of healthy participants (SYNCH1PP-ASYNCH1PP: mean = -7.41e-03, sd ± = 0.09, p = 0.257; SYNCH1PP-ASYNCH3PP: mean = 0.02, sd ± = 0.07, p = 0.295; ASYNCH1PP-ASYNCH3PP: mean = 0.03, sd ± = 0.11, p = 0.438). These data show that the patient was sensitive to our experimental manipulation, showing a similar modulation of the SoA as healthy participants.

The patient was well aware of her memory deficits, for which she had been tested repeatedly in her neuropsychological examinations and memory rehabilitation sessions. Although we initially tested the patient under incidental encoding, she admitted she was expecting to be tested on her memory in the task, therefore, we compared her performance with participants who performed the task under intentional encoding instruction (Experiment 3). Inspection of **Figure 7C** showed that, despite her preserved SoA, she did not have higher recognition performance in the SYNCH1PP condition compared to the other two conditions (as healthy participants; see **Figure 2D**). Instead, she displayed the opposite pattern (**Figure 7C**), showing the lowest recognition performance in the SYNCH1PP condition (accuracy of 58% correct) compared to the other two conditions (with visuomotor and perspectival incongruency), having an accuracy of 73% correct answers in ASYNCH1PP and 66% correct answers in ASYNCH3PP. Comparing her recognition performance with those of healthy participants (Experiment 3), the patient differed significantly when comparing SYNCH1PP-ASYNCH1PP (mean = 0.06, sd ± = 0.11, p = 0.036; the comparison SYNCH1PP-ASYNCH3PP was not significantly different compared to healthy participants (mean = 0.06, sd ± = 0.13, p = 0.148).
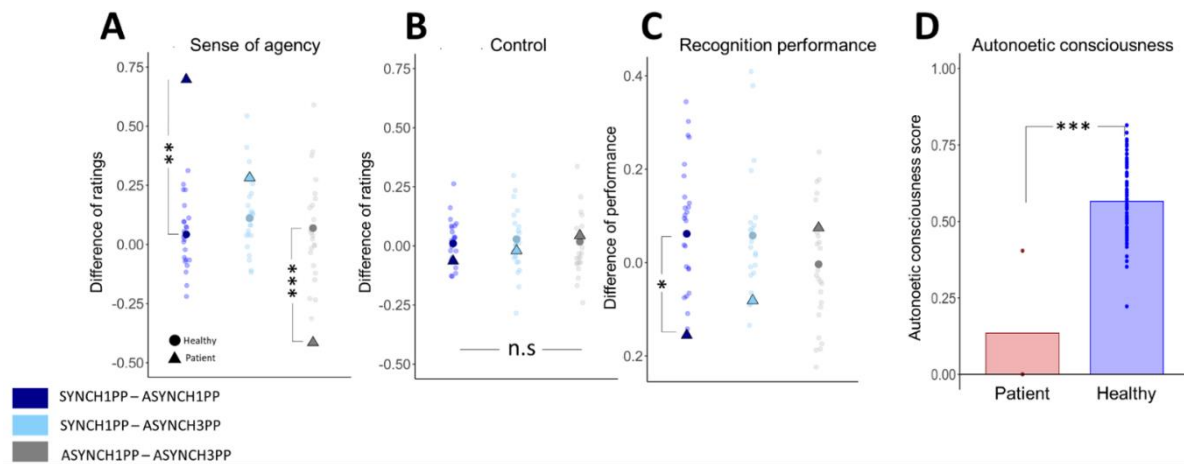
*Figure 7: Successful SoA manipulation but decreased recognition performance under visuomotor and perspectival congruency with amnestic patient. A. Higher SoA under visuomotor and perspectival congruency. The patient had high SoA under visuomotor and perspectival congruency and lower SoA under visuomotor and perspectival incongruency. The difference SYNCH1PP-ASYNCH1PP (dark blue) and ASYNCH1PP-ASYNCH3PP (grey) are significantly higher than healthy participants (N = 24) as tested with a Crawford test. **,*** indicates significance level with p-value <0.01 and <0.001 respectively. B. No difference in ratings in the control patient for the patient compared to participants. The patient had low ratings for control questions which did not differ between conditions and were not different from healthy participants (N = 24). C. Worst recognition performance under visuomotor and perspectival congruency in the patient with bilateral lesion of hippocampi. The recognition performance of the patient is lower under visuomotor and perspectival congruency compared to visuomotor and perspectival incongruency. The recognition performance under visuomotor and perspectival congruency (SYNCH1PP) is significantly lower when compared to visuomotor mismatch (ASYNCH1PP) between the patient (triangle) and healthy participants (colored dots; Experiment 3; N = 24) as tested with a Crawford test. * indicates significance level with p-value <0.05. D. lower autonoetic consciousness in amnestic patient compared to healthy participants. The patient was able to remember only the scene encoded under the strongest visuomotor and perspectival incongruency (ASYNCH3PP). The autonoetic consciousness of the patient (red) was lower compared to healthy participants (blue; Experiment 3; N= 24) as tested with a Crawford test. *** indicates significance level with p-value <0.001.*

To provide further evidence for an impairment of changes in EM, based on visuomotor and perspectival congruency, we investigated autonoetic consciousness in the patient, that is, her ability to re-experience the sensory and perceptual details of an event (A. Gardiner et al., 2001; Piolino et al., 2003; Tulving, 1985). For this, we employed several questions assembled from the memory characteristics questionnaire (MCQ; Johnson et al., 1988), the episodic autobiographical memory interview (Irish et al., 2011), and the "affected limb intentional feeling questionnaire" (ALEFq; Crema et al., 2022; see Supplementary text for more detail). Autonoetic consciousness is predominantly tested for autobiographical real-life events, but here, we were interested in testing her autonoetic consciousness for the three virtual 3D scenes into which she was immersed during the encoding session. In particular, we were interested in whether her autonoetic consciousness would differ across the three encoding conditions. Based on her lower recognition performance in the SYNCH1PP condition, we predicted that she would indicate lower autonoetic consciousness scores in this condition. Autonoetic consciousness was tested one week after encoding and confirmed this prediction. Strikingly, the patient was only able to remember the scene encoded in 3PP (ASYNCH3PP: *"the cabin"*) but not able even to evoke either scene involving the 1PP (i.e., SYNCH1PP: *"living*

room"; ASYNCH1PP: *"Changing room").* Although we presented pictures of the empty scene encoded in the two latter conditions, the patient could not remember any aspects of the scenes. The patient reported: *"I can remember seeing the cabin, all in wood, and my arm moving in the scene, but I have never seen this living room nor this changing room"*. Critically, we did not show the picture of the scene in ASYNCH3PP to help her recollect the information, showing that the retrieval of this scene was possible and easier than of the two others. Accordingly, she was not able to answer and rate the different questions of the ANC questionnaire related to SYNCH1PP and ASYNCH1PP. However, we note that her overall rating score in the autonoetic consciousness questionnaire for the ASYNCH3PP scene was still low (**Figure 7D**). The patient was able to remember the virtual scene but rated her memory for the global vividness of the scene as vague (second last choice on a scale from 1 to 7) and global re-experience as 25% (second last choice on the scale). The averaged ratings significantly differed from the scores of healthy participants as tested with a Crawford test (mean = 0.57, sd = 0.12, p <0.001).

Collectively, these behavioral results show that a patient with severe amnesia and normal SoA performed worse when remembering objects that were shown in a scene encoded under visuomotor and perspectival congruency. Her performance differed and showed the opposite effect than healthy participants. This was extended by our analysis of autonoetic consciousness, revealing that the patient was not able to relive and re-experience complex 3D scenes that she encoded from a 1PP, but only some elements encoded in the condition with maximal visuomotor and perspectival incongruency (ASYNCH3PP). The patient suffered damage to bilateral hippocampi (and adjacent structures), and our analysis showed that her damage involved the left hippocampal region found in our fMRI analysis in healthy participants (performing the same tasks) and linked to visuomotor and perspectival congruency using RSA and ERS analysis. There was no damage to PMC or the SMA, shown to be involved in the present visuomotor and perspectival effects on the SoA. Accordingly, we argue that the abnormal effect of visuomotor and perspectival congruency on recognition performance in the present patient was caused by damage to the left hippocampus and/or a disruption of the anatomical-functional connections between the left hippocampus and PMC, confirming and extending the data obtained in Experiments 1-3.

2.4 Discussion

In this study, we investigated the neural mechanisms linking BSC and EM and specifically targeted the process of reinstatement of brain activity at encoding during recognition.

We found that participants had a higher recognition performance under unmanipulated BSC (visuomotor and perspectival congruency) when the encoding was intentional. Consistent with previous empirical evidence, we found that hippocampal reinstatement correlated with recognition performance and showed that it was decreased by an alteration of BSC at encoding. Third, we found that hippocampal reinstatement correlated with the reinstatement of cortical areas responsive to BSC alterations during encoding for scenes encoded under visuomotor and perspectival congruency. Finally, we observed a reverse pattern of recognition performance in an amnestic patient with bilateral lesions in the hippocampus and adjacent regions. Our results suggest that BSC plays an integral part in the formation and retrieval of information encoded in EM through the mechanism of hippocampal reinstatement.

We report how altered BSC significantly decreased participants' recognition performance under intentional encoding instructions. Other studies have observed this drop in performance when manipulating BSC perspective (Bergouignan et al., 2014; Bréchet et al., 2019) and body ownership (Iriye & Ehrsson, 2022) under incidental encoding instruction. Interestingly, we did not find a difference between conditions in the recognition performance under incidental encoding instructions (Experiments 1 and 2). We speculate that this absence of difference was due to increased task difficulty in the incidental instruction, thus increasing our results' signal to noise ratio. Another possibility to explain this difference is that the movement of the right upper limb performed by the participants disrupted participant's attention thus increasing the task difficulty. As the encoding was intentional in Experiment 3, the effect of BSC is therefore stronger because not disrupted by this factor. However, previous studies showed that the neural mechanism behind incidental and intentional encoding are similar (Haese & Czernochowski, 2015; Téllez-Alanís & Cansino, 2004). Therefore, in this study, we interpreted the neural changes observed in Experiment 2 (performed under incidental instruction) as relevant for both incidental and intentional encoding.

At the neural level, hippocampal reinstatement of encoding activity was correlated with participants' recognition performance, consistent with previous studies (Liang and Preston, 2017; Tompary et al., 2016). In line with the reinstatement framework, we interpret this metric as a correlate of the successful remobilization of encoded information during recognition. Critically, we observed a higher reinstatement in the condition with preserved BSC (visuomotor and perspectival congruency) compared to the altered BSC conditions in the left hippocampus. This result provides for the first time evidence of the impact of BSC on the neural mechanism of EM taking into account both encoding and retrieval processes. We also observed a difference in the reinstatement of the left MTG, as reported in previous EM studies

(Oedekoven et al., 2017). However, MTG was not correlated with recognition performance, suggesting that hippocampus reinstatement is a specific neural proxy for memory. We propose to explain the absence of a relationship between MTG and recognition performance with the hierarchical organization of the medial temporal lobe, in which the hippocampus is at the top, receiving only highly integrated neural signals (Lavenex & Amaral, 2000; Shimamura, 2010; Shimamura & Wickens, 2009; Squire et al., 2004). Therefore, we can speculate that the manipulation of BSC modulates the reinstatement of different parts of the medial temporal lobe, which ultimately reverberates in hippocampus reinstatement.

According to the MTT, the hippocampus indexes the sensory information of a memory stored in the cortex (Moscovitch et al., 2005; Nadel et al., 2000; Sekeres et al., 2017). A few studies have demonstrated an association between hippocampus activity at encoding and reactivation of cortical regions at retrieval (Goode et al., 2020; Staresina et al., 2013). Moreover, silencing hippocampus activity in mice at retrieval prevented the reactivation of cortical areas involved during encoding processes (Tanaka et al., 2014). Our results showed a coupling between hippocampus reinstatement and brain regions sensitive to our BSC manipulation (left dPMC and left SMA). dPMC and SMA have been reported as brain regions sensitive to SoA manipulation and sensitive to sensorimotor manipulation (Charalampaki et al., 2022; Rabellino et al., 2018; Seghezzi, Giannini, et al., 2019; Tsakiris et al., 2010). This indicates that our BSC manipulation during encoding triggered neural changes during the encoding of the event. Interestingly, the coupling of the left hippocampus with the left dPMC was observed only under visuomotor and perspectival congruency, suggesting that it depends on preserved BSC state (visuomotor and perspectival congruency). We propose that this association depends on a congruent sensorimotor integration during the encoding of an event.

Although deficit of EM was described in several single case studies (Klein and Nichols, 2012; Levine et al., 1998; Piolino et al., 2003; Scoville and Milner, 1957, St-Laurent et al., 2014), to our knowledge, the link between EM deficit and BSC was not investigated in these reports. In our study, the patient showed spared semantic memory and deficit in EM for autobiographical events. Her fungal infection and the resulting bilateral lesions in hippocampi and adjacent regions triggered this deficit. This dichotomy between EM deficit and spared semantic memory is consistent with the MTT, in which the hippocampus plays a critical role in the recollection of EM deficit while semantic memory is stored in the cortex which is not lesioned in our patient (Moscovitch et al., 2016; Nadel et al., 2000; Sekeres et al., 2017).

Our results showed that the patient did not seem to display alteration of BSC as her SoA ratings were in the same direction as SoA manipulation in healthy population (Grivaz et al., 2017; Haggard, 2017; Padilla-Castañeda et al., 2014; Weijs et al., 2021) and similar to the healthy participants tested in this study. However, when testing the amnestic patient with the same recognition task as the one we used on healthy participants, we found an opposite pattern of recognition performance. Notably, the patient performed above the chance level in each condition, suggesting that the reverse pattern of performance is less likely to be coincidental.

We expected the patient to rely more on bodily cues and therefore have an enhanced difference between the condition with visuomotor and perspectival congruency. Instead, we found that the patient was better under altered BSC states (visuomotor and perspectival incongruency). This was further confirmed one week later when the patient could only retrieve the information of the subjective reliving of the scene encoded under the strongest BSC alteration (ASYNCH3PP). As we found BSC- sensitive hippocampal reinstatement when testing healthy participants, we speculated that the patient's hippocampal lesions could affect hippocampus reinstatement necessary to retrieve EM encoded under preserved BSC. This was further supported by the overlap of the patient's lesion and the data-driven hippocampus identification on healthy participants. This proposition also implies that EM encoded under altered BSC states (visuomotor and perspectival incongruency), relies on different neural substrates for their retrieval. The retrieval of autobiographical memory relies more on functional connectivity between the hippocampus and parahippocampus as opposed to the retrieval of overgeneral memory and public events, thought to depend on functional connectivity between MTG and temporal pole (Maguire et al., 2000). Therefore, one can speculate that events encoded under altered BSC states are more likely attributed to overgeneral memory than events encoded under preserved BSC, more personal and closer to autobiographical memory. Future studies should thus investigate the different neural substrates underlying EM retrieval of events encoded under altered BSC states and how they relate to different memory contents.

This study is not without limitations: We were not able to record the gaze pattern of participants during the encoding of the virtual scenes, as such a device was not compatible with the stereoscopic goggles. Therefore, we could not provide a substantial measure to compare the different gaze directions that the difference in conditions could have triggered. Participants may have paid more attention to their right arm when encoded under visuomotor and perspectival mismatch, thus decreasing recognition performance when tested one hour later in the recognition task. Nevertheless, our control analysis on objects' laterality did not show any interaction between conditions and the objects' side, suggesting that the right hand's movement might have shifted the attention to the right equally in all conditions. These results support that our findings are more likely due to modulation of BSC than attentional effect.

Additionally, this study did not aim to separate the specific mechanism associated with perspective shift and asynchrony. Instead, we build it graded, using light (ASYNCH1PP) and substantial BSC alteration (ASYNCH3PP). The fMRI experiment was long (in total 2x 1h30 plus 1h of break), so the graded design was the best ratio between time and explanatory power. Increasing the length of the study may have increased the overall difficulty, which we suspected to have reduced the behavioral effect on memory performance in the incidental encoding task. Therefore future studies should investigate the difference between perspective shift and asynchrony on the neural mechanism underlying BSC and EM association.

To conclude, this study highlights the role of BSC on the encoding of EM. The use of immersive virtual reality and motion tracking systems enabled to test EM under conditions as close as possible to encoding in real life. We showed that manipulating BSC at encoding gives rise to behavioral and neural changes in EM retrieval. We propose for the first time that this association is held at the neural level through the mechanism of hippocampus reinstatement. Our results align with the MTT, linking EM with cortical areas, and add to this framework the necessity of preserved BSC states to successfully associate BSC with EM retrieval.

2.5 Methods

Participants

In Experiment 1, 26 participants (7 male; mean age 23 ± 3.4 years) took part in the study, in Experiment 2, 29 participants (11 male, 3 gender-nonconforming, mean age 24 ± 3.4 years) and in Experiment 3, 27 participants (10 male, mean age 27 ± 3.5). All participants were right-handed as tested by the FLANDERS (Flinders Handedness Survey; FLANDERS, Grimshaw, 2013) and reported no history of neurological or psychiatric disorder and no drug consumption in the 48h hours preceding the experiment. All participants were compensated for their participation and provided written informed consent following the local ethical committee (Cantonal Ethical Committee of Geneva: 2015-00092, and Vaud and Valais: 2016-02541) and the declaration of Helsinki (2013).

Patient

In Experiment 4, we tested a 62 years old female patient (french speaker, right-handed) suffering from moderate to severe retrograde amnesia and moderate anterograde amnesia following fungal brain infection. The patient had specific deficit in autobiographical memory, more specifically in the episodic content, as tested by neuropsychologists from the hospital. The patient had bilateral lesions in the hippocampus and adjacent regions (amygdala, parahippocampus, see **Figure 5**). The patient suffered from severe epileptic crises, which were reduced in intensity and frequency after a few months. The patient provided written inform consent following the local ethical committee (Cantonal Ethical Committee of Geneva: 2015-00092, and Vaud and Valais: 2016-02541) and the declaration of Helsinki (2013).

Neuropsychological assessment

In Experiment 4, the patient was tested by trained neuropsychologists from the hospital to assess the potential impairment in different cognitive domain three months after her infection. The neuropsychologist found that the patient did not suffered from confabulation as tested with the confabulation battery (Dalla Barba et al., 2018). The patient showed normal working memory and semantic memory (tested with Wechsler memory scale and Camel and cactus test ; Wechsler, 2008; Moore et al., 2022). The patient had deficit in delayed recall of episodic memory (Van der Linden et al., 2006; Wilson et al., 2008, 2010), and memory for public events (Puel et al., 2016). Critically, her autobiographical memory was the most affected (TEMPau test ; Piolino et al., 2008)[1].

A trained neuropsychologist from our lab tested the patient three months after Experiment 4, to obtain a clinical profile closer to the period when she participated to the experiment. The

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[1] *We are still waiting on the raw neuropsychological data from the hospital*

patient performed within the normal range for the episodic memory task (Rey Auditory Verbal Learning test, Rey, 1941). She had no deficit in executive function as tested with the frontal assessment battery and the trail making test (Dubois et al., 2000, Reitan & Wolfson, 1985). She showed a deficit in episodic autobiographical memory during the autobiographical fluency test as compared to semantic autobiographical memory which was not different from the normal range (Dritschel et al., 1992).

Immersive virtual reality with motion tracking

Immersive virtual reality

The VR paradigm and the visual stimuli were inspired and adapted from former works on EM research using immersive VR (Bréchet et al., 2019; Gauthier et al., 2020; Iriye & St. Jacques, 2021). Particular care was given to the progressive VR immersion procedure to build a strong experience of presence in the virtual environments (Herbelin et al., 2016; Slater, 2009) and to maintain it throughout the experiment. Because the immersion in VR of participant lying in an MRI scanner is particularly challenging, we based our approach on the work of (Gauthier et al., 2021), including the methods of familiarization with the virtual environment, and embodiment into a virtual body representation (Kilteni et al., 2012).

To improve the reproducibility of our paradigm, all instructions were fully automatized and provided by audio recordings through headphones. We ensured that instructions were both heard and understood during the familiarization session.

VR display

Participants were visually immersed in VR using either a head-mounted display (Oculus Rifts S, refreshing rate 80Hz, resolution 1280 x 1440 per eye, 660 ppi; Experiments 1, 3 and 4) or MRI-compatible goggles composed of two full-HD resolution displays (1920 x 1200, 16:10 WUXGA) allowing stereoscopic rendering at 60 Hz with a diagonal field of view of 60° (Experiment 2; Visual System HD, NordicNeuroLab, Bergen, Norway).

Motion Tracking

In Experiments 1 and 3, participants were lying down in a mock Magnetic Resonance (MR) scanner and holding custom response devices in their hands. The custom-made response device consisted of two hand-held tennis balls with integrated buttons and reflective 6-degree-of-freedom motion trackers to simultaneously maintain stable and avatar-consistent hand postures, track arm motion, and record participants' answers during the in-scanner questions. Participants were wearing gloves with Velcro tape ensuring a static position of the response devices to the hand to avoid any issue related to tracker rotation and its related visual rendering in the virtual environment. We used three motion tracking cameras (Qualisys Oqus 500+m cameras with 180 Hz, 4 MegaPixel resolution) to track the devices.

In Experiment 2, participants were lying down in the MR scanner. We used a similar setup as described in (Gauthier et al., 2021). To summarize, the same tracking system is used but it is provided by six motion-tracking cameras attached to the ceiling of the MRI room to avoid any movement of the camera during the experiment and optical artifacts.

In Experiment 4, the patient was sitting on a chair, with her legs resting on a second chair in front of her, to keep the position and field of view of the scenes as similar as possible compared to the healthy participants tested in Experiments 1,2 and 3. The patient was wearing the same custom-made device used in healthy participants (Experiments 1,2,3) with the same hand position. However, because we tested the patient in another location where the motion tracking system described previously was not available, we used LEAP motion (2 cameras and 3 infrared LEDs) to track the patient's movement.

Software

Immersion paradigms and experimental procedures were implemented using ExVR (ExVR; Lance Florian (2019), GitHub repository: https://github.com/BlankeLab/ExVR). ExVR is a solution for designing and executing VR experiments that uses the Unity 3D engine (https://unity.com/) to perform visual rendering with realistic lighting and shading. Following principles similar to Psychopy (https://www.psychopy.org/), ExVR graphical interface allows creating complex scenes, controlling experimental variables with complex randomizations, generating logs and exporting result data compatible with standard analysis software. Additionally, for Experiment 2, ExVR also enabled the synchronization of MRI acquisition with VR experimental data.

Experimental design

All experiments consisted of three separate main sessions. The first session was a memory encoding session, which was followed by an assessment of bodily self-consciousness (BSC; see below). The last session was a recognition session carried out one hour later (**Figure 1**). We also assessed autonoetic consciousness one week after the encoding session. Before the experiment, all participants underwent a familiarization session with VR for each of the four scenes (the three encoding scenes and the BSC assessment scene) that were used during the task (See Supplementary method).

Encoding session

During the encoding session, participants were instructed to keep moving their right arm while observing a virtual avatar animated in real-time. Arm movements were instructed to occur between two virtual black spheres that were displayed in the visual scene. The black spheres were aligned vertically, to the right of the virtual body, and placed at the level of the avatar's hip (**Figure 1**). We manipulated the sense of agency (SoA ; David et al., 2008; Haggard, 2017; Haggard and Chambon, 2012) of participants by exposing them to three different scenes

(Supplementary video 1) corresponding to the three different experimental conditions, which were characterized by different levels of sensorimotor synchrony. For this, participants were exposed to different levels of visuomotor congruency between the movement of their right arm and the shown movements of the avatar's arm in the virtual scene (i.e. (Galvan Debarba et al., 2018; Kannape & Blanke, 2013). In the SYNCH1PP condition there was no visuomotor manipulation thus, the virtual avatar was seen from a first-person perspective (1PP) and the right virtual arm was moving synchronously to the participant's arm movements (SYNCH1PP). In the ASYNCH1PP condition, the virtual avatar was also seen from a 1PP, but was moving with a visuomotor delay that varied between 800-1000 ms to the movement of the participant (ASYNCH1PP). In a third, control, condition (ASYNCH3PP), the avatar was seen from a third-person perspective (3PP) and was moving with a visuomotor delay that varied between 800-1000 ms with respect to the movement of the participant. For the 3PP the body of the avatar was moved forward in the virtual scene to maintain the same visual angle of all objects in the scene, as compared to the other experimental conditions. Based on previous work on the SoA (Debarba et al., 2017; Kokkinara et al., 2016; Longo & Haggard, 2009), we expected stronger SoA in the condition with no visuomotor manipulation and naturalistic perspective (SYNCH1PP) compared to the conditions with visuomotor manipulation (ASYNCH1PP and ASYNCH3PP).

Each of the three encoded scenes contained eighteen objects and was associated with a specific experimental condition (SYNCH1PP, ASYNCH1PP, ASYNCH3PP) for each participant. This association between the encoded scene and experimental condition was pseudo-randomized across participants. For each experimental condition, each scene was presented for 30 seconds and repeated four times. An inter-trial interval consisting of a fixation cross appeared for five seconds in between each scene presentation to avoid potential carry-over effects from one condition to another.

Encoding was incidental in Experiments 1, 2 and 4. Thus, participants were not told that they participated in a memory experiment and that their object recognition was going to be tested. Encoding was intentional in Experiment 3 and we instructed the participants to pay close attention to the scene during encoding and told them they would be tested on the scene one hour later. The rest of the experimental design was similar between Experiments 1, 2 and 3.

BSC assessment

Immediately after the encoding session, participants were immersed in a different outdoor scene containing eighteen new objects to avoid any memory interference with the encoding of the 3 scenes associated with the 3 experimental conditions. They were instructed to perform the same right arm movements and were observing the same avatar in SYNCH1PP, ASYNCH1PP, and ASYNCH3PP, but now performed in the outdoor environment (duration 30 seconds). Based on previous BSC work, in Experiments 1, 2 and 3, we also included a response to a threat stimulus directed towards the avatar (i.e. after 30 seconds, an unexpected event

consisting in a virtual knife seen as approaching the avatar's trunk (Petkova and Ehrsson, 2008; Moon et al., 2022).

Participants had to rate their agreement with five statements regarding different aspects of BSC: (Q1) "I felt that I was controlling the virtual body" to rate their SoA toward the movement of the virtual avatar; (Q2) "I felt that the virtual body was mine" to rate their level of body ownership toward the virtual avatar intentionally; (Q3, only in Experiment 1,2 and 3) "I was afraid to be hurt by the knife" to rate their threat response as a proxy of the subjective measure of their BSC as in (Moon et al., 2022). We also included two control statements for experimental bias: (Q4) "I felt like I had more than three bodies" and (Q5) "I felt like the trees were my body". The five statements were presented successively and in a randomized order. For each statement, a cursor was programmed to move between the two extreme points of the presented agreement scale (between 0 to 1, with an increment of 0.001) at a constant speed. The participant had to stop it at the desired position by a left button press and then validate their response with a right button press. Before validation, the participant was free to retry indefinitely to specify his agreement level by a left click until being satisfied by the answer. The BSC assessment was repeated twice per condition.

Recognition session

One hour after the encoding session, participants were presented with the encoded scenes again. Participants were exposed to each tested scene for 10 seconds and were then asked to respond yes or no to the question: "Is there any change in the room compared to the first time you saw it?". They were instructed just before the start of the recognition session that they will have to answer concerning the original scenes seen during the encoding session. Some of these scenes were identical to the encoded scenes (original scene), and other were modified (changed scene). Participants performed 45 trials per condition. Among those 45 trials, 20 trials corresponded to the presentation of the original scene and 20 trials corresponded to a modified version of the original scene in which one single object was changed in either color or shape. There were 5 additional attentional trials in which two to three objects were changing shape, color, or position in the scene. The attentional trials were used to incite the participants to carefully observe the entire scene instead of simply trying to spot a single object change. Attentional trials were not included in the analysis. Importantly, during the recognition session, participants did not move their arms and no avatar was shown to not modulate BSC during the recognition session. In Experiment 1, following the first statement participants had to answer an additional question: "How confident are you about your answer?". They had to answer using the same cursor-stopping scheme as in the BSC assessment following the encoding session. In Experiments 2,3 and 4, the second question was replaced by a 3-second fixation cross, to reduce experimental time as well as to avoid carry-over effects.

Autonoetic consciousness session

We also tested the patient and the healthy participants' autonoetic consciousness for each condition, at one week after the encoding. Autonoetic consciousness was assessed using an association of questions from a well-established questionnaire for a total of 31 questions, including questions from the "Memory characteristic questionnaire" (19 questions, Johnson et al., 1998), part B of the "Episodic autobiographic memory interview" (EAMI; 8 questions; (Irish et al., 2011), two questions from the "affected limb intentional feeling questionnaire" (ALEFq; Crema et al., 2022) and one additional question related to our research question ("I remember the movement and gesture I was doing with my body during the event", ordinal scale, See Supplementary table 31 for a list of all the questions). In Experiments 1, 2 and 3, participants answered the questionnaire by phone (to minimize drop-out rate, also to minimize close contact with participants due the covid pandemic). In Experiment 4, there were no pandemic-related restrictions and the patient filled the questionnaire in the experimenter's presence, also to ensure that all questions were well understood. We measured autonoetic consciousness for each condition for each participant and the patient.

MRI acquisition

MR images were acquired using a 3T MRI scanner (MAGNETOM PRISMA; Siemens) using a 64-channel head coil at Campus Biotech Geneva. Each participant underwent a 5 min anatomical imaging using a T1-weighted MPRAGE sequence (TR = 2300 ms, TE = 2.25 ms, TI = 900 ms, Slice thickness = 1 mm, In-plane resolution = 1 mm × 1 mm, Number of slices = 208, FoV = 256 mm, Flip angle = 8). Encoding, BSC assessment, and recognition sessions were acquired with a whole-brain T2*-weighted Echo Planar Imaging (EPI) sequence (TR = 1500 ms, TE = 30 ms, 69 slices, flip-angle = 50°, Slice thickness = 2 mm, In-plane resolution = 2 mm × 2 mm, Multiband factor = 2, slice acquisition order = interleaved). B0 field maps were acquired during both the first and the second acquisition to correct EPI distortion due to magnetic field inhomogeneity.

MRI preprocessing

MRI data were preprocessed with SPM12 v7487 (http://www.fil.ion.ucl.ac.uk/spm). Voxel displacement maps for the first and second sessions were calculated for each subject using pre-subtracted Phase and Magnitude Images (Short and Long echo times = 4.92 and 7.38 ms respectively, Blip direction = -1, total EPI readout time = 34.72 ms) using standard parameters. Functional images were then realigned to the first image of each session and unwarped using the voxel displacement maps with standard parameters. Images were then slice-timed to correct for time delay due to volume acquisition time using slice acquisition times recovered from DICOM raw images. Anatomical images were segmented using the unified segmentation approach (Ashburner & Friston, 2005). Functional images were corrected for bias field and then coregistered with bias field-corrected segmented anatomy using normalized mutual

information. Finally, coregistered functional images were normalized using the normalization parameters estimate during unified segmentation of the anatomical images.

For the univariate GLMs specification, the functional images were smoothed using a FWHM Gaussian smoothing kernel of 5 mm. For the representational similarity analysis, we used a 2 mm-Kernel to balance spatial pattern information preservation and noise reduction (Misaki et al., 2013).

Categorical and trial-by-trial (TBT) General Linear Models (GLM)

Multivariate and univariate analyses used contrast maps based on subject-level random effect GLMs specified and estimated using SPM12. GLMs were estimated based on a design matrix that covered four fMRI sessions (scene encoding, BSC assessment, and two runs of scene recognition) and included boxcar regressors convolved with a canonical hemodynamic response function.

For the categorical GLM, the regressors covered the conditions of interest, nuisance covariates, and sessions. The conditions of interest for the encoding run were the 3 encoding conditions (4 × 30 s each): ENC-SYNCH1PP, ENC-ASYNCH1PP, and ENC-ASYNCH3PP, the inter-trial interval baselines (ENC-BASE, 12 × 5 s), the familiarization runs (4 × 15 s), the arm movement familiarization runs (3 × 30 s) for each of the 3 conditions, the in-scanner question familiarization runs (self-paced), and the button presses (0 s). The conditions of interest for BSC assessments were the 3 runs (2 × 30 s each) similar to encoding in an independent scene: BSC-SYNCH1PP, BSC-ASYNCH1PP, and BSC-ASYNCH3PP, the knife event for each condition (3 s each), the BSC questions (5 questions repeated twice, self-paced), one run (30 s) of arm movement without any visual stimuli, the inter-trial interval baselines (ENC_BASE, 12 × 5 s), and the button presses. For each of the recognition runs, we modeled each combination of condition, success/failure and stimulus presentation (original/changed scene) as separate regressors (for instance, REC_SYNCH1PP_Change_Success would be one possible regressor) leading to 12 possible regressors (10 s each). Attentional trials were modeled as separate regressors following the same logic (for instance, REC_SYNCH1PP_Change_Success_Catch would be one possible regressor) leading to 4 possible regressors (self-paced). The questions were modeled the same way as separate regressors. In total, for each recognition run, 32 possible regressors were modeled. Finally, similarly to other runs, we modeled inter-trial interval baselines (REC_BASE, 135 × 3 s) and button presses. The nuisance covariates were rigid translation of the head in x, y, and z direction as well as roll, pitch and yaw rotation. Finally, we added a regressor modeling individual frames exceeding 0.5 mm of framewise displacement (Power et al., 2014) to regress out frames altered by excessive head movement.

We removed two participants from our MRI analysis because of excessive head movement (more than 15% of the volumes exceeding a threshold of 0.5 mm framewise displacement).

For the TBT GLM, we used the same regressors for encoding and BSC assessment as the categorical GLM but modeled each recognition trial as a single regressor to fit better statistical models of the activity and to account for possible neural repetition suppression effects.

Participant-wise GLMs were estimated for all voxels inside a common gray matter mask (SPM gray matter tissue probability map exceeding a 0.25 threshold). A high-pass filter (128 s cutoff) was applied to remove slow drifts unrelated to the paradigm.

BSC univariate analyses

To quantify the impact of BSC manipulation on brain activity, we used a two-level analysis scheme in SPM12. From first-level contrast maps, we built a second-level within-subject ANOVA model including the three BSC conditions and derived the group-level contrasts: 2*SYNCH1PP − (ASYNCH1PP+ASYNCH3PP) to identify brain regions that were significantly activated by visuomotor and perspectival congruency compared to the other conditions. For whole-brain exploration of the effects, we used a cluster-defining threshold of $p < 0.001$ uncorrected combined with (1) a False Discovery Rate (FDR) cluster-level correction with a threshold of $p < 0.05$ to account for multiple comparisons. We then parcellated the cluster onto three different ROIs using the automated anatomical labeling atlas (aal; Tzourio-Mazoyer et al., 2002).

Encoding-recognition representational similarity analysis (RSA)

To identify the brain regions displaying similar modulations of brain activity with respect to the conditions during the scene encoding and scene recognition sessions, we performed a searchlight representational similarity analysis (RSA) in a liberal gray matter mask (voxel with more than 25% of being gray matter based on SPM tissue probability maps, within an 8mm sphere (RSA; Kriegeskorte et al., 2008; Kriegeskorte et al., 2006). For each participant, each session, and each voxel, we created brain representational dissimilarity matrices (bRDM) by computing the Euclidean distance between these conditions (**Figure 3A**). We obtained a 3 × 3 matrix with 0 in the diagonal, corresponding to the distance of the condition with itself (i.e., ENC-SYNCH1PP compared to ENC-SYNCH1PP), and with the Euclidean distance of the conditions in the rest of the matrix (i.e., ENC-SYNCH1PP compared to ENC-ASYNCH1PP; **Figure 3A**). We then computed the similarity (Z-Fisher transform of Spearman rank correlation) between the encoding bRDM and recognition bRDM for each voxel, providing an RSA brain map for each participant. Finally, we performed a permutation test by shuffling the similarity score of participants to obtain a normal distribution and select the voxel displaying significant neural similarity at a threshold of $p < 0.05$ with a cluster size bigger than 500 voxels (**Figure 3B**).

Encoding-recognition similarity analysis (ERS)

To investigate the level of neural patterns of reinstatement between encoding and recognition specifically to each condition, we computed the encoding-recognition similarity score in regions of interest selected by both searchlight RSA and univariate GLM. The ERS was computed as the Pearson correlation between vectorized neural activities corresponding (1) to encoding activity and (2) to recognition activity, for each of the conditions: SYNCH1PP, ASYNCH1PP, and ASYNCH3PP (**Figure 3C**). It is worth mentioning that this approach is distinct from the encoding-recognition RSA: while the RSA provides a second-order isomorphism between encoding and recognition condition-related pattern, i.e., a measure of the *between-conditions* neural similarity, the ERS provides a direct linear *within-condition* similarity. Thus, while we can expect that some regions display both kinds of similarity, it is not necessarily the case by design.

We first used simple GLMs contrast maps for the calculation of ERS and refine it further using TBT GLMs.

ERS as predictors of recognition performance

We used (R Core Team, 2022) and R studio (RStudio, 2022) for the analysis reported below. Linear mixed models were computed using the package *lme4* (Walker et al., 2015) and *modelsummary* to create table from linear mixed model results and obtain the significativity threshold (p-value) associated with each dependent variable (Bundock, 2022).

To better understand the effect of conditions on ERS we used a linear mixed model approach with ERS as dependent variable (continuous) explained by conditions (3 levels: SYNCH1PP, ASYNCH1PP and ASYNCH3PP) and trials (fixed effect, continuous), with participants added as random effect and SYNCH1PP as intercept condition of the model. We applied the model separately on successful and failed trials based on our priori hypothesis that the possible effect would mainly be seen for successful trials (i.e., when the memory trace is successfully reinstated).

We used a linear mixed model approach to investigate the link between recognition performance (percentage of correct answers, dependent variable) and ERS (we extracted ERS for success and failure separately but use the average between success and failure when there was no significant difference between those two). We first compared the model with and without conditions and selected the model with lowest AIC and passing a $\chi 2$ test (alpha = 0.05) compared to the previous model. We then derived p-values for individual effects Bonferroni corrected from the selected final model with LmerTest package.

To refine further the estimation of the relationship between recognition performance and ERS, we used a mixed effect logistic regression to explain TBT recognition performance (dependent variable, binary) as a function of conditions (fixed, 3 levels: SYNCH1PP, ASYNCH1PP and ASYNCH3PP), ERS (fixed, continuous) and stimulus presented (2 levels, original or changed scene) including their interaction for each of our ROI. We first compared

the model with and without stimulus conditions and selected the model with lowest AIC and passing a χ 2 test (alpha = 0.05) compared to the previous model. We then derived p-values for individual effects from the selected final model with LmerTest package for which we added participants as a random effect and used SYNCH1PP condition as the intercept of the model.

Finally, to investigate the link between hippocampal ERS and neocortical ERS in regions indexing agency manipulation, we applied a linear mixed model with hippocampal ERS (dependent variable) as a function of conditions (fixed effect, 3 levels: SYNCH1PP, ASYNCH1PP and ASYNCH3PP), neocortical ERS (fixed, continuous) and trial number (fixed, continuous) to model habituation effects. We estimated one linear mixed model for each neocortical ERS, we then derived p-values for individual effects from the selected final model with LmerTest package for which we added participants as a random effect and used SYNCH1PP condition as the intercept of the model. We corrected the interaction results for the number of regions using a Bonferroni procedure.

Behavioral data analysis

BSC and recognition performance

Recognition performance was analyzed separately for healthy participants performing Experiments 1 and 2 (incidental encoding) and for healthy participants performing Experiment 3 (intentional encoding). Behavorial analysis was applied using R (R Core Team, 2022) and R studio (RStudio, 2022) to analyze the behavorial data. Linear mixed models were computed using the package *lme4* (Walker et al., 2015) and *modelsummary* to create table from linear mixed model results and obtain the significativity threshold (p-value) associated with each dependent variable (Bundock, 2022).

BSC ratings

To verify that our experimental manipulation (during encoding) impacted the SoA, we used a linear mixed model with SoA ratings as dependent variable (continuous) explained by the conditions as a factor with three levels (SYNCH1PP, ASYNCH1PP, ASYNCH3PP) and participant as a random effect. The SYNCH1PP condition was used as the intercept condition for all our models. For the analysis of the incidental encoding, we added the experiment as a fixed factor (two levels: Experiment 1 and Experiment 2) to ensure there was no main difference of results between experiments. As the BSC assessment for each condition was repeated twice, we used the average rating. We report the main results in the text and all detailed tables for our mixed model can be seen in the Supplementary table section (Supplementary table 1-4 and 7-10). We used the same linear mixed modeling to investigate the effect of our experimental manipulation on body ownership, control, and threat ratings. For the control questions, we averaged the ratings of the two control questions together. For the threat item, we used only the first round of ratings as dependent variable as the habituation effect was strong and is well referenced in literature (Boroomand-Tehrani et al., 2020; Weijs et al., 2021).

We removed 3 participants from Experiment 1 and 2 participants from Experiment 2 due to tracking issues during BSC assessment or high ratings in the control questions which were explained by a misunderstanding of the questions by participants as revealed during post experiments feedback at the end of the recognition session. We also removed two participants from Experiment 3 because of technical issues during the experiment. Those participants were therefore not included in our BSC analysis as well as in the recognition performance analysis. We thus included a total of 76 participants across the three experiments for our BSC assessment analysis (24 Experiment 1, 27 Experiment 2, 25 Experiment 3).

Recognition performance

To investigate if the experimental manipulation during encoding led to different levels of performance during the recognition task, we applied a mixed effect logistic regression with the binary performance score of participants as the dependent variable explained by conditions as fixed factor with three levels (SYNCH1PP, ASYNCH1PP, ASYNCH3PP) as well as the scene as a factor with three levels (ENV1, ENV2, ENV3). We added participants as a random effect and used the SYNCH1PP condition as reference condition. We used Experiment 1 as the intercept condition for our model of incidental encoding instruction and added the experiment as a factor of two levels (Experiment 1 and Experiment 2) to ensure there was no main effect of experiments. We report the main results in the text and all detailed tables for our mixed model can be seen in the Supplementary text, table section (Supplementary table 5-6 and 11-12). For a better visualization of the recognition performance on the figures, we plotted the recognition performance as the percent of correct answer given in the task per conditions.

To better understand whether the right upper limb movement of the participants had an effect on participant's performance, we investigated the separated performance of participants when the objects change was on the left, versus right side of the virtual avatar. We applied a linear mixed model to explain the recognition performance (binary), with the conditions as a fixed factor with three levels (SYNCH1PP, ASYNCH1PP, ASYNCH3PP) and an interaction with the object side as a factor with two level (LEFT,RIGHT). We added the scene as a factor with three levels (ENV1,ENV2,ENV3) and the participants as a random factor. We used SYNCH1PP as the reference condition.

We removed two participants from Experiment 1, two for Experiment 2 and one for Experiment 3 because they had performance below 50% or always answered yes during the recognition task. We thus included a total of 72 participants across the three experiments for our analysis on recognition performance (22 Experiment 1, 26 Experiment 2, 24 Experiment 3).

Patient data

In this section, we describe the analysis performed on the data of the patient with autobiographical memory deficits caused by bilateral medial temporal lobe damage.

Behavorial analysis

For data from Experiment 4, we used a Crawford test to compare the patient's BSC ratings between the three experimental conditions the ratings of healthy participants and applied the test for the three comparisons (SYNCH1PP-ASYNCH1PP, SYNCH1PP-ASYNCH3PP and ASYNCH1PP-ASYNCH3PP). We carried out the same analysis to compare the difference of recognition performance between conditions of the patient with the recognition performance of healthy participants (Crawford test applied on the three comparison SYNCH1PP-ASYNCH1PP, SYNCH1PP-ASYNCH3PP and ASYNCH1PP-ASYNCH3PP). Although the patient had an incidental encoding similar to Experiment 1 and 2, we compared her recognition performance with healthy participants who encoded the task under intentional encoding instruction (Experiment 3), because she was aware of her deficit and knew she would be tested on memory.

Autonoetic consciousness

We first reversed the scale of three questions extracted from the EAMI questionnaire (Q1: " How often would you estimate you have thought about this memory since it first occurred"; Q2: " How often would you estimate you have spoken about this memory since it first occurred? "; Q3: "When you recall this event how would you describe it in terms of vividness? This can apply to the richness of sights, sounds, smells, tastes, touch, and any movements you may have made.") to have higher ratings corresponding to stronger recollection (the original EAMI questionnaire associate the lowest ratings, 1, as strong vividness and 7 a slow vividness for example). Original scaling is depicted in black in Supplementary Table 32, and reversed scaling in green.

To quantify the difference of autonoetic consciousness between the patient and the young healthy participants from Experiment 3, we computed an autonoetic consciousness score for each participant and each condition, by suming the normalized ratings of the questionnaire together, to obtain one score per participant per condition. We then applied a Crawford test between the average autonoetic consciousness score of the patient between conditions, with the average autonoetic consciousness score across conditions of participants from Experiment 3.

2.6 References

Aspell, J. E., Lenggenhager, B., & Blanke, O. (2009). Keeping in Touch with One's Self : Multisensory Mechanisms of Self-Consciousness.

  PLOS ONE, *4*(8), e6488. https://doi.org/10.1371/journal.pone.0006488

Bergouignan, L., Nyberg, L., & Ehrsson, H. H. (2014). Out-of-body–induced hippocampal amnesia. *Proceedings of the National Academy of*

  Sciences, *111*(12), 4421-4426. https://doi.org/10.1073/pnas.1318801111

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature Reviews Neuroscience*, *13*(8), Art. 8.

  https://doi.org/10.1038/nrn3292

Blanke, O., & Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. *Trends in Cognitive Sciences*, *13*(1), 7-13.

  https://doi.org/10.1016/j.tics.2008.10.003

Blanke, O., Slater, M., & Serino, A. (2015). Behavioral, Neural, and Computational Principles of Bodily Self-Consciousness. *Neuron*, *88*(1),

  145-166. https://doi.org/10.1016/j.neuron.2015.09.029

Boccia, M., Teghil, A., & Guariglia, C. (2019). Looking into recent and remote past : Meta-analytic evidence for cortical re-organization of

  episodic autobiographical memories. *Neuroscience & Biobehavioral Reviews*, *107*, 84-95.

  https://doi.org/10.1016/j.neubiorev.2019.09.003

Boroomand-Tehrani, A., Huntley, A. H., Jagroop, D., Campos, J. L., Patterson, K. K., Tremblay, L., & Mansfield, A. (2020). The effects of

  postural threat induced by a virtual environment on performance of a walking balance task. *Human Movement Science*, *74*,

  102712. https://doi.org/10.1016/j.humov.2020.102712

Bosch, S. E., Jehee, J. F. M., Fernández, G., & Doeller, C. F. (2014). Reinstatement of Associative Memories in Early Visual Cortex Is Signaled

  by the Hippocampus. *Journal of Neuroscience*, *34*(22). https://doi.org/10.1523/JNEUROSCI.0805-14.2014

Botvinick & Cohen. (1998). *Rubber hands 'feel' touch that eyes see | Nature*. https://www.nature.com/articles/35784

Bréchet, L., Hausmann, S. B., Mange, R., Herbelin, B., Blanke, O., & Serino, A. (2020). Subjective feeling of re-experiencing past events using

  immersive virtual reality prevents a loss of episodic memory. *Brain and Behavior*, *10*(6), e01571.

  https://doi.org/10.1002/brb3.1571

Bréchet, L., Mange, R., Herbelin, B., Theillaud, Q., Gauthier, B., Serino, A., & Blanke, O. (2019). First-person view of one's body in immersive

  virtual reality : Influence on episodic memory. *PLoS ONE*, *14*(3), Art. 3. https://doi.org/10.1371/journal.pone.0197763

Burgess, N., Maguire, E. A., & O'Keefe, J. (2002). The Human Hippocampus and Spatial and Episodic Memory. *Neuron*, *35*(4), 625-641.

  https://doi.org/10.1016/S0896-6273(02)00830-9

Cabeza, R., Dolcos, F., Prince, S. E., Rice, H. J., Weissman, D. H., & Nyberg, L. (2003). Attention-related activity during episodic memory

  retrieval : A cross-function fMRI study. *Neuropsychologia*, *41*(3), 390-399. https://doi.org/10.1016/S0028-3932(02)00170-7

Charalampaki, A., Ninija Karabanov, A., Ritterband-Rosenbaum, A., Bo Nielsen, J., Roman Siebner, H., & Schram Christensen, M. (2022).

  Sense of agency as synecdoche : Multiple neurobiological mechanisms may underlie the phenomenon summarized as sense of

  agency. *Consciousness and Cognition*, *101*, 103307. https://doi.org/10.1016/j.concog.2022.103307

Crema, A., Bassolino, M., Guanziroli, E., Colombo, M., Blanke, O., Serino, A., Micera, S., & Molteni, F. (2022). Neuromuscular electrical

  stimulation restores upper limb sensory-motor functions and body representations in chronic stroke survivors. *Med*, *3*(1), 58-

  74.e10. https://doi.org/10.1016/j.medj.2021.12.001

Dalla Barba, G., Brazzarola, M., Barbera, C., Marangoni, S., Causin, F., Bartolomeo, P., & Thiebaut de Schotten, M. (2018). Different patterns of confabulation in left visuo-spatial neglect. *Experimental Brain Research*, *236*(7), 2037-2046. https://doi.org/10.1007/s00221-018-5281-8

Danker, J. F., Tompary, A., & Davachi, L. (2017). Trial-by-Trial Hippocampal Encoding Activation Predicts the Fidelity of Cortical Reinstatement during Subsequent Retrieval. *Cerebral Cortex*, *27*(7), Art. 7. https://doi.org/10.1093/cercor/bhw146

Daselaar, S. M., Rice, H. J., Greenberg, D. L., Cabeza, R., LaBar, K. S., & Rubin, D. C. (2008). The Spatiotemporal Dynamics of Autobiographical Memory : Neural Correlates of Recall, Emotional Intensity, and Reliving. *Cerebral Cortex*, *18*(1), 217-229. https://doi.org/10.1093/cercor/bhm048

David, N., Newen, A., & Vogeley, K. (2008). The "sense of agency" and its underlying cognitive and neural mechanisms. *Social Cognition, Emotion, and Self-Consciousness*, *17*(2), 523-534. https://doi.org/10.1016/j.concog.2008.03.004

De Vignemont, F. (2011). A Self for the Body. *Metaphilosophy*, *42*(3), 230-247. https://doi.org/10.1111/j.1467-9973.2011.01688.x

Debarba, H. G., Bovet, S., Salomon, R., Blanke, O., Herbelin, B., & Boulic, R. (2017). Characterizing first and third person viewpoints and their alternation for embodied interaction in virtual reality. *PLOS ONE*, *12*(12), e0190109. https://doi.org/10.1371/journal.pone.0190109

Dijkstra, K., Kaschak, M. P., & Zwaan, R. A. (2007). Body posture facilitates retrieval of autobiographical memories. *Cognition*, *102*(1), 139-149. https://doi.org/10.1016/j.cognition.2005.12.009

Dinh, H. Q., Walker, N., Hodges, L. F., Song, C., & Kobayashi, A. (1999). Evaluating the importance of multi-sensory input on memory and the sense of presence in virtual environments. *Proceedings IEEE Virtual Reality (Cat. No. 99CB36316)*, 222-228. https://doi.org/10.1109/VR.1999.756955

Ehrsson, H. H. (2007). The Experimental Induction of Out-of-Body Experiences. *Science*, *317*(5841), 1048-1048. https://doi.org/10.1126/science.1142175

Ehrsson, H. H. (2012). The Concept of Body Ownership and Its Relation to Multisensory Integration. In B. E. Stein (Éd.), *The New Handbook of Multisensory Processing* (p. 775-792). The MIT Press. https://doi.org/10.7551/mitpress/8466.003.0067

Fourneret, P., & Jeannerod, M. (1998). Limited conscious monitoring of motor performance in normal subjects. *Neuropsychologia*, *36*(11), 1133-1140. https://doi.org/10.1016/S0028-3932(98)00006-2

Frank et al. (2001). *Defective Recognition of One's Own Actions in Patients With Schizophrenia | American Journal of Psychiatry*. https://ajp.psychiatryonline.org/doi/full/10.1176/appi.ajp.158.3.454

Galvan Debarba, H., Boulic, R., Salomon, R., Blanke, O., & Herbelin, B. (2018). Self-attribution of distorted reaching movements in immersive virtual reality. *Computers & Graphics*, *76*, 142-152. https://doi.org/10.1016/j.cag.2018.09.001

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

Gauthier, B., Albert, L., Martuzzi, R., Herbelin, B., & Blanke, O. (2021). Virtual Reality Platform for Functional Magnetic Resonance Imaging in Ecologically Valid Conditions. *Proceedings of the 27th ACM Symposium on Virtual Reality Software and Technology*. https://doi.org/10.1145/3489849.3489894

Gauthier, B., Bréchet, L., Lance, F., Mange, R., Herbelin, B., Faivre, N., Bolton, T. A. W., Ville, D. V. D., & Blanke, O. (2020). First-person body view modulates the neural substrates of episodic memory and autonoetic consciousness : A functional connectivity study. *NeuroImage*, *223*, 117370. https://doi.org/10.1016/j.neuroimage.2020.117370

Goode, T. D., Tanaka, K. Z., Sahay, A., & McHugh, T. J. (2020). An Integrated Index : Engrams, Place Cells, and Hippocampal Memory. *Neuron*, *107*(5), 805-820. https://doi.org/10.1016/j.neuron.2020.07.011

Gordon, A. M., Rissman, J., Kiani, R., & Wagner, A. D. (2014). Cortical Reinstatement Mediates the Relationship Between Content-Specific Encoding Activity and Subsequent Recollection Decisions. *Cerebral Cortex*, *24*(12), 3350-3364. https://doi.org/10.1093/cercor/bht194

Grimshaw,G.M, N., M. E. (2013). *The Flinders Handedness survey (FLANDERS) : A brief measure of skilled hand preference | Elsevier Enhanced Reader*. https://doi.org/10.1016/j.cortex.2013.02.002

Grivaz, P., Blanke, O., & Serino, A. (2017). Common and distinct brain regions processing multisensory bodily signals for peripersonal space and body ownership. *NeuroImage*, *147*, 602-618. https://doi.org/10.1016/j.neuroimage.2016.12.052

Haese, A., & Czernochowski, D. (2015). Sometimes we have to intentionally focus on the details : Incidental encoding and perceptual change decrease recognition memory performance and the ERP correlate of recollection. *Brain and Cognition*, *96*, 1-11. https://doi.org/10.1016/j.bandc.2015.02.003

Haggard, P. (2017). Sense of agency in the human brain. *Nature Reviews Neuroscience*, *18*(4), Art. 4. https://doi.org/10.1038/nrn.2017.14

Haggard, P., & Chambon, V. (2012). Sense of agency. *Current Biology: CB*, *22*(10), R390-2.

Herbelin, B., Salomon, R., Serino, A., & Blanke, O. (2016). 5. Neural Mechanisms of Bodily Self-Consciousness and the Experience of Presence in Virtual Reality. In *5. Neural Mechanisms of Bodily Self-Consciousness and the Experience of Presence in Virtual Reality* (p. 80-96). De Gruyter Open Poland. https://doi.org/10.1515/9783110471137-005

Ionta, S., Gassert, R., & Blanke, O. (2011). Multi-Sensory and Sensorimotor Foundation of Bodily Self-Consciousness – An Interdisciplinary Approach. *Frontiers in Psychology*, *2*. https://www.frontiersin.org/articles/10.3389/fpsyg.2011.00383

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

Iriye, H., & Ehrsson, H. H. (2022). Perceptual illusion of body-ownership within an immersive realistic environment enhances memory accuracy and re-experiencing. *IScience*, *25*(1), 103584. https://doi.org/10.1016/j.isci.2021.103584

Iriye, H., & Jacques, P. L. S. (2018). *Construction and Elaboration of Autobiographical Memories from Multiple Visual Perspectives* (p. 317594). bioRxiv. https://doi.org/10.1101/317594

Iriye, H., & St. Jacques, P. L. (2021). Memories for third-person experiences in immersive virtual reality. *Scientific Reports*, *11*(1), Art. 1. https://doi.org/10.1038/s41598-021-84047-6

Jeannerod, M. (2007). Being oneself. *Journal of Physiology-Paris*, *101*(4), 161-168. https://doi.org/10.1016/j.jphysparis.2007.11.005

Johnson, M. K., Foley, M. A., Suengas, A. G., & Raye, C. L. (1988). Phenomenal characteristics of memories for perceived and imagined autobiographical events. *Journal of Experimental Psychology: General*, *117*, 371-376. https://doi.org/10.1037/0096-3445.117.4.371

Kannape, O. A., & Blanke, O. (2013). Self in motion : Sensorimotor and cognitive mechanisms in gait agency. *Journal of Neurophysiology*, *110*(8), 1837-1847. https://doi.org/10.1152/jn.01042.2012

Kannape, O. A., Schwabe, L., Tadi, T., & Blanke, O. (2010). The limits of agency in walking humans. *Neuropsychologia*, *48*(6), 1628-1636.

    https://doi.org/10.1016/j.neuropsychologia.2010.02.005

Kensinger, E. A., & Ford, J. H. (2020). Retrieval of Emotional Events from Memory. *Annual Review of Psychology*, *71*(1), 251-272.

    https://doi.org/10.1146/annurev-psych-010419-051123

Kilteni, K., Groten, R., & Slater, M. (2012). The Sense of Embodiment in Virtual Reality. *Presence: Teleoperators and Virtual Environments*,

    21(4), 373-387. https://doi.org/10.1162/PRES_a_00124

Klein, S. B., & Nichols, S. (2012). Memory and the Sense of Personal Identity. *Mind*, *121*(483), 677-702.

    https://doi.org/10.1093/mind/fzs080

Kokkinara, E., Kilteni, K., Blom, K. J., & Slater, M. (2016). First Person Perspective of Seated Participants Over a Walking Virtual Body Leads

    to Illusory Agency Over the Walking. *Scientific Reports*, *6*(1), 28879. https://doi.org/10.1038/srep28879

Kriegeskorte, N., Mur, M., & Bandettini, P. (2008). Representational similarity analysis—Connecting the branches of systems neuroscience.

    Frontiers in Systems Neuroscience, *2*. https://www.frontiersin.org/article/10.3389/neuro.06.004.2008

Kriegeskorte Nikolaus, Goebel Rainer, & Bandettini Peter. (2006). Information-based functional brain mapping. *Proceedings of the National

    Academy of Sciences*, *103*(10), 3863-3868. https://doi.org/10.1073/pnas.0600244103

Lavenex, P., & Amaral, D. G. (2000). Hippocampal-neocortical interaction : A hierarchy of associativity. *Hippocampus*, *10*(4), 420-430.

    https://doi.org/10.1002/1098-1063(2000)10:4<420::AID-HIPO8>3.0.CO;2-5

Lenggenhager, B., Mouthon, M., & Blanke, O. (2009). Spatial aspects of bodily self-consciousness. *Consciousness and Cognition*, *18*(1),

    110-117. https://doi.org/10.1016/j.concog.2008.11.003

Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video Ergo Sum : Manipulating Bodily Self-Consciousness. *Science*, *317*(5841),

    1096-1099. https://doi.org/10.1126/science.1143439

Levine, B., Black, S. E., Cabeza, R., Sinden, M., Mcintosh, A. R., Toth, J. P., Tulving, E., & Stuss, D. T. (1998). Episodic memory and the self in a

    case of isolated retrograde amnesia. *Brain*, *121*(10), 1951-1973. https://doi.org/10.1093/brain/121.10.1951

Liang, J. C., & Preston, A. R. (2017). Medial temporal lobe reinstatement of content-specific details predicts source memory. *Cortex, 91*,

    67-78. https://doi.org/10.1016/j.cortex.2016.09.011

Longo, M. R., & Haggard, P. (2009). Sense of Agency Primes Manual Motor Responses. *Perception*, *38*(1), 69-78.

    https://doi.org/10.1068/p6045

Mack, M. L., & Preston, A. R. (2016). Decisions about the past are guided by reinstatement of specific memories in the hippocampus and

    perirhinal cortex. *NeuroImage*, *127*, 144-157. https://doi.org/10.1016/j.neuroimage.2015.12.015

Maguire, E. A., Mummery, C. J., & Büchel, C. (2000). Patterns of hippocampal-cortical interaction dissociate temporal lobe memory

    subsystems. *Hippocampus*, *10*(4), 475-482. https://doi.org/10.1002/1098-1063(2000)10:4<475::AID-HIPO14>3.0.CO;2-X

Misaki, M., Luh, W.-M., & Bandettini, P. A. (2013). The effect of spatial smoothing on fMRI decoding of columnar-level organization with

    linear support vector machine. *Journal of Neuroscience Methods*, *212*(2), 355-361.

    https://doi.org/10.1016/j.jneumeth.2012.11.004

Moon, H.-J., Gauthier, B., Park, H.-D., Faivre, N., & Blanke, O. (2022). Sense of self impacts spatial navigation and hexadirectional coding in

    human entorhinal cortex. *Communications Biology*, *5*(1), Art. 1. https://doi.org/10.1038/s42003-022-03361-5

Moscovitch, M., Cabeza, R., Winocur, G., & Nadel, L. (2016). Episodic Memory and Beyond : The Hippocampus and Neocortex in Transformation. *Annual review of psychology*, *67*, 105-134. https://doi.org/10.1146/annurev-psych-113011-143733

Moscovitch, M., Rosenbaum, R. S., Gilboa, A., Addis, D. R., Westmacott, R., Grady, C., McAndrews, M. P., Levine, B., Black, S., Winocur, G., & Nadel, L. (2005). Functional neuroanatomy of remote episodic, semantic and spatial memory : A unified account based on multiple trace theory. *Journal of Anatomy*, *207*(1), 35-66. https://doi.org/10.1111/j.1469-7580.2005.00421.x

Nadel, L., Samsonovich, A., Ryan, L., & Moscovitch, M. (2000). Multiple trace theory of human memory : Computational, neuroimaging, and neuropsychological results. *Hippocampus*, *10*(4), 352-368. https://doi.org/10.1002/1098-1063(2000)10:4<352::AID-HIPO2>3.0.CO;2-D

Nigro, G., & Neisser, U. (1983). Point of view in personal memories. *Cognitive Psychology*, *15*(4), 467-482. https://doi.org/10.1016/0010-0285(83)90016-6

Oedekoven, C. S. H., Keidel, J. L., Berens, S. C., & Bird, C. M. (2017). Reinstatement of memory representations for lifelike events over the course of a week. *Scientific Reports*, *7*(1), Art. 1. https://doi.org/10.1038/s41598-017-13938-4

Pacheco Estefan, D., Sánchez-Fibla, M., Duff, A., Principe, A., Rocamora, R., Zhang, H., Axmacher, N., & Verschure, P. F. M. J. (2019). Coordinated representational reinstatement in the human hippocampus and lateral temporal cortex during episodic memory retrieval. *Nature Communications*, *10*(1), Art. 1. https://doi.org/10.1038/s41467-019-09569-0

Padilla-Castañeda, M. A., Frisoli, A., Pabon, S., & Bergamasco, M. (2014). The Modulation of Ownership and Agency in the Virtual Hand Illusion under Visuotactile and Visuomotor Sensory Feedback. *Presence*, *23*(2), 209-225. https://doi.org/10.1162/PRES_a_00181

Park, H.-D., & Blanke, O. (2019). Coupling Inner and Outer Body for Self-Consciousness. *Trends in Cognitive Sciences*, *23*(5), 377-388. https://doi.org/10.1016/j.tics.2019.02.002

Petkova, V. I., & Ehrsson, H. H. (2008). If I Were You : Perceptual Illusion of Body Swapping. *PLOS ONE*, *3*(12), e3832. https://doi.org/10.1371/journal.pone.0003832

Petkova, V., Khoshnevis, M., & Ehrsson, H. H. (2011). The Perspective Matters ! Multisensory Integration in Ego-Centric Reference Frames Determines Full-Body Ownership. *Frontiers in Psychology*, *2*. https://www.frontiersin.org/articles/10.3389/fpsyg.2011.00035

Petrides, M. (2007). The Orbitofrontal Cortex : Novelty, Deviation from Expectation, and Memory. *Annals of the New York Academy of Sciences*, *1121*(1), 33-53. https://doi.org/10.1196/annals.1401.035

Pfeiffer, C., Grivaz, P., Herbelin, B., Serino, A., & Blanke, O. (2016). Visual gravity contributes to subjective first-person perspective. *Neuroscience of Consciousness*, *2016*(1). https://doi.org/10.1093/nc/niw006

Piolino, P., Desgranges, B., Belliard, S., Matuszewski, V., Lalevée, C., De La Sayette, V., & Eustache, F. (2003). Autobiographical memory and autonoetic consciousness : Triple dissociation in neurodegenerative diseases. *Brain*, *126*(10), 2203-2219. https://doi.org/10.1093/brain/awg222

Power, J. D., Mitra, A., Laumann, T. O., Snyder, A. Z., Schlaggar, B. L., & Petersen, S. E. (2014). Methods to detect, characterize, and remove motion artifact in resting state fMRI. *NeuroImage*, *84*, 320-341. https://doi.org/10.1016/j.neuroimage.2013.08.048

Rabellino, D., Burin, D., Harricharan, S., Lloyd, C., Frewen, P. A., McKinnon, M. C., & Lanius, R. A. (2018). Altered Sense of Body Ownership and Agency in Posttraumatic Stress Disorder and Its Dissociative Subtype : A Rubber Hand Illusion Study. *Frontiers in Human Neuroscience*, *12*. https://www.frontiersin.org/articles/10.3389/fnhum.2018.00163

Rand, G., & Wapner, S. (1967). Postural status as a factor in memory. *Journal of Verbal Learning and Verbal Behavior*, *6*(2), 268-271. https://doi.org/10.1016/S0022-5371(67)80107-5

Ritchey, M., Wing, E. A., LaBar, K. S., & Cabeza, R. (2012). Neural Similarity Between Encoding and Retrieval is Related to Memory Via Hippocampal Interactions. *Cerebral Cortex*, *23*(12), Art. 12. https://doi.org/10.1093/cercor/bhs258

Ritchey, M., Wing, E. A., LaBar, K. S., & Cabeza, R. (2013). Neural Similarity Between Encoding and Retrieval is Related to Memory Via Hippocampal Interactions. *Cerebral Cortex*, *23*(12), 2818-2828. https://doi.org/10.1093/cercor/bhs258

Rolls, E. T. (2022). The hippocampus, ventromedial prefrontal cortex, and episodic and semantic memory. *Progress in Neurobiology*, *217*, 102334. https://doi.org/10.1016/j.pneurobio.2022.102334

Salomon, R., Kannape, O. A., Debarba, H. G., Kaliuzhna, M., Schneider, M., Faivre, N., Eliez, S., & Blanke, O. (2022). Agency Deficits in a Human Genetic Model of Schizophrenia : Insights From 22q11DS Patients. *Schizophrenia Bulletin*, *48*(2). https://doi.org/10.1093/schbul/sbab143

Schacter, D. L., Guerin, S. A., & St. Jacques, P. L. (2011). Memory distortion : An adaptive perspective. *Trends in Cognitive Sciences*, *15*(10), 467-474. https://doi.org/10.1016/j.tics.2011.08.004

Scoville, W. B., & Milner, B. (1957). LOSS OF RECENT MEMORY AFTER BILATERAL HIPPOCAMPAL LESIONS. *Journal of Neurology, Neurosurgery, and Psychiatry*, *20*(1), 11-21.

Seghezzi, S., Giannini, G., & Zapparoli, L. (2019). Neurofunctional correlates of body-ownership and sense of agency : A meta-analytical account of self-consciousness. *Cortex*, *121*, 169-178. https://doi.org/10.1016/j.cortex.2019.08.018

Sekeres, M. J., Moscovitch, M., & Winocur, G. (2017). Mechanisms of Memory Consolidation and Transformation. In N. Axmacher & B. Rasch (Éds.), *Cognitive Neuroscience of Memory Consolidation* (p. 17-44). Springer International Publishing. https://doi.org/10.1007/978-3-319-45066-7_2

Shimamura, A. P. (2010). Hierarchical relational binding in the medial temporal lobe : The strong get stronger. *Hippocampus*, *20*(11), 1206-1216. https://doi.org/10.1002/hipo.20856

Shimamura, A. P., & Wickens, T. D. (2009). Superadditive memory strength for item and source recognition : The role of hierarchical relational binding in the medial temporal lobe. *Psychological Review*, *116*, 1-19. https://doi.org/10.1037/a0014500

Slater, M. (2009). Place illusion and plausibility can lead to realistic behaviour in immersive virtual environments. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1535), 3549-3557. https://doi.org/10.1098/rstb.2009.0138

Squire, L. R., Stark, C. E. L., & Clark, R. E. (2004). The Medial Temporal Lobe. *Annual Review of Neuroscience*, *27*(1), 279-306. https://doi.org/10.1146/annurev.neuro.27.070203.144130

St. Jacques, P. L. (2019). A New Perspective on Visual Perspective in Memory. *Current Directions in Psychological Science*, *28*(5), 450-455. https://doi.org/10.1177/0963721419850158

St. Jacques, P. L., Szpunar, K. K., & Schacter, D. L. (2017). Shifting visual perspective during retrieval shapes autobiographical memories. *NeuroImage*, *148*, 103-114. https://doi.org/10.1016/j.neuroimage.2016.12.028

Staresina, B. P., Cooper, E., & Henson, R. N. (2013). Reversible Information Flow across the Medial Temporal Lobe : The Hippocampus Links Cortical Modules during Memory Retrieval. *Journal of Neuroscience*, *33*(35), 14184-14192. https://doi.org/10.1523/JNEUROSCI.1987-13.2013

Staresina, B. P., Henson, R. N. A., Kriegeskorte, N., & Alink, A. (2012). Episodic Reinstatement in the Medial Temporal Lobe. *Journal of Neuroscience*, *32*(50), 18150-18156. https://doi.org/10.1523/JNEUROSCI.4156-12.2012

Tanaka, K. Z., Pevzner, A., Hamidi, A. B., Nakazawa, Y., Graham, J., & Wiltgen, B. J. (2014). Cortical Representations Are Reinstated by the Hippocampus during Memory Retrieval. *Neuron*, *84*(2), 347-354. https://doi.org/10.1016/j.neuron.2014.09.037

Téllez-Alanís, B., & Cansino, S. (2004). Incidental and intentional encoding in young and elderly adults. *NeuroReport*, *15*(11), 1819-1823. https://doi.org/10.1097/01.wnr.0000137075.41257.98

Tompary, A., Duncan, K., & Davachi, L. (2016). High-resolution investigation of memory-specific reinstatement in the hippocampus and perirhinal cortex. *Hippocampus*, *26*(8), 995-1007. https://doi.org/10.1002/hipo.22582

Tsakiris, M. (2010). My body in the brain : A neurocognitive model of body-ownership. *Neuropsychologia*, *48*(3), 703-712. https://doi.org/10.1016/j.neuropsychologia.2009.09.034

Tsakiris, M., Longo, M. R., & Haggard, P. (2010). Having a body versus moving your body : Neural signatures of agency and body-ownership. *Neuropsychologia*, *48*(9), 2740-2749. https://doi.org/10.1016/j.neuropsychologia.2010.05.021

Tulving, E. (1972). Episodic and semantic memory. In *Organization of memory* (p. xiii, 423-xiii, 423). Academic Press.

Tulving, E. (1985). Memory and consciousness. *Canadian Psychology / Psychologie canadienne*, *26*, 1-12. https://doi.org/10.1037/h0080017

Tulving, E., & Markowitsch, H. J. (1998). Episodic and declarative memory : Role of the hippocampus. *Hippocampus*, *8*(3), 198-204. https://doi.org/10.1002/(SICI)1098-1063(1998)8:3<198::AID-HIPO2>3.0.CO;2-G

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., Mazoyer, B., & Joliot, M. (2002). Automated Anatomical Labeling of Activations in SPM Using a Macroscopic Anatomical Parcellation of the MNI MRI Single-Subject Brain. *NeuroImage*, *15*(1), 273-289. https://doi.org/10.1006/nimg.2001.0978

Weijs, M. L., Macartney, E., Daum, M. M., & Lenggenhager, B. (2021). Development of the bodily self : Effects of visuomotor synchrony and visual appearance on virtual embodiment in children and adults. *Journal of Experimental Child Psychology*, *210*, 105200. https://doi.org/10.1016/j.jecp.2021.105200

Wheeler. (2000). *Memory's echo : Vivid remembering reactivates sensory-specific cortex | PNAS*. https://www.pnas.org/doi/abs/10.1073/pnas.97.20.11125

Wing, E. a, Marsh, E. J., & Cabeza, R. (2013). Neural correlates of retrieval-based memory enhancement : An fMRI study of the testing effect. *Neuropsychologia*, *51*(12), Art. 12. https://doi.org/10.1016/j.neuropsychologia.2013.04.004

Wing, E. A., Ritchey, M., & Cabeza, R. (2015). Reinstatement of Individual Past Events Revealed by the Similarity of Distributed Activation Patterns during Encoding and Retrieval. *Journal of Cognitive Neuroscience*, *27*(4), 679-691. https://doi.org/10.1162/jocn_a_00740

Xiao, X., Dong, Q., Gao, J., Men, W., Poldrack, R. A., & Xue, G. (2017). Transformed Neural Pattern Reinstatement during Episodic Memory Retrieval. *Journal of Neuroscience*, *37*(11), 2986-2998. https://doi.org/10.1523/JNEUROSCI.2324-16.2017

Yamamoto, T., Yamada, K., Nishimura, T., & Kinoshita, S. (2005). Tractography to Depict Three Layers of Visual Field Trajectories to the Calcarine Gyri. *American Journal of Ophthalmology*, *140*(5), 781-785.e1. https://doi.org/10.1016/j.ajo.2005.05.018

2.7 Supplementary information

Experimental design

Familiarization

We performed a familiarization in two steps. First, immediately after entering the mock scanner (Experiment 1 and 3) or the MR scanner (Experiment 2), we made sure participants could hear the instructions given in the headset (Experiment 1 and 3) and the headphone (Experiment2). We also asked participants to perform the arm movement while displaying an empty scene in the forest and gave feedback in case the movement were too fast. This part was important for participants to get used to the movement of the arm inside the MRI and make sure they would not touch the MRI boundaries with their arm during the experiment.

Second, prior to the encoding session, participants were immersed in the four scenes (three encoding scenes and the BSC scene) but emptied from all the objects being part of the later recognition task. They were instructed to move their hands and observe the scene for 15 seconds after which they were asked one binary question "2 plus 2 equal 4" where they had to answer if this statement was correct or not, followed by a second question "How confident are you about your answer ?" to train for the two types of questions that would be asked during the experiment. Finally, they were asked to move their right arm for 30 seconds to train them for the rest of the experiment. During this time, when necessary, we interacted with the participant to tell them if the movement was too fast or not having an amplitude big enough. We used participant's mother tongue to give the instruction when it was possible (French and English, French translations are given in supp mat) otherwise we used English. Each participant started the familiarization in the BSC scenes in the SYNCH1PP condition. The familiarization of the encoding scenes was performed in the same conditions as the one they would encode during the experiment.

Visuomotor and perspectival congruency during incidental encoding and object recognition (behavior, Experiment 1 and 2)

Effect of scenes on recognition performance

We also compared the effect of recognition performance between scenes to ensure that each scene had the same level of difficulty. We found that scene 2 was significantly easier compared to the two other scenes in incidental encoding , Experiment 1 and 2; estimate = 0.22, z = 3.33, p = 0.001) but not in intentional encoding (Experiment 3 ; estimate = 0.013, z = 0.12, p = 0.9). Therefore, we included the scene as fixed effect in our analysis to take this bias into account. However, since the association between condition and scene was pseudorandomized between participants this effect should not affect our findings.

ERS analysis. Reinstatement of encoding activity in the left hippocampus is higher for visuomotor and perspectival congruency and index recognition memory.

Model selection to explain recognition performance with hippocampal ERS

To better understand the link between hippocampal ERS and memory, we compared a model which explains recognition performance using hippocampal ERS and conditions (Model 1) with a model considering only hippocampal ERS irrespective of conditions (Model 0). We found that both models were equally good (i.e. had the same AIC; m1 AIC = -159.83, m0 AIC = -159.73, X_2= 8.10, p = 0.088, Supplementary table 26). Therefore we used the model with the smaller number of parameters (Model 0) for further analysis.

Hippocampal ERS and performance, Trial-by-Trial

The positive correlation between left hippocampal ERS and recognition performance was found for average hippocampal ERS (per session average of successful and failed trials) and for the overall recognition performance (percent of correct answers). To investigate whether this relation holds for single trials, we applied a logistic mixed effect model to investigate trial-by-trial recognition performance with trial-by-trial hippocampal ERS (as described in the main text). This analysis revealed a significant triple interaction between condition, stimulus (same scene than the one at encoding versus changed scene), and left hippocampal ERS, when SYNCH1PP was compared to ASYNCH3PP (estimate = -2.04, z = -2.6, p = 0.009, Supplementary table 27-29). P*ost-hoc* analysis revealed that the significant effect was driven by the significantly positive relationship between recognition performance and left hippocampal ERS in SYNCH1PP (**Figure 4B,** Supplementary table 30), but only when the stimulus presented was the same scene as the one observed at encoding (estimate = 1.7, z = 3.5, p <0.001). The relation between hippocampal ERS and recognition performance was not significant for the ASYNCH3PP conditions (Supplementary table 31).This shows that only the main experimental condition with visuomotor and perspectival congruency, associated activity in left hippocampus with recognition performance on a trial by trial basis.

Hippocampal-neocortical interactions revealed by ERS are modulated by visuomotor and perspectival congruency

We found that participant's SoA was correlated with the activity of the BSC regions at encoding (Premotor left: r = 0.22, df = 79, t = 1.98, p = 0.05, right SMA: r = 0.35, df = 79, t = 3.38, p = 0.0001, r = 0.3, df = 79, t = 2.81, p = 0.006 , suggesting that these regions identified using the contrast (SYNCH1PP > ASYNCH1PP +ASYNCH3PP) are involved in the subjective outcome of the BSC manipulation (SoA).

Amnestic patient with bilateral hippocampal damage is impaired in recognizing objects encoded with visuomotor and perspectival congruency

The patient tested in Experiment 4 had an increase sensitivity to our experimental manipulation when comparing SYNCH1PP with ASYNCH1PP condition. The SoA difference between SYNCH1PP and ASYNCH3PP was not significantly different compared to healthy participants but going in the same direction (SYNCH1PP-ASYNCH3PP: mean = 0.08, sd ± = 0.18, p = 0.134). For the ownership ratings, she had a significantly increased difference, going in the similar direction than the healthy participants (Ownership:SYNCH1PP-ASYNCH1PP: mean = 4.00e-03, sd ± = 0.21, p = 0.002). The other difference were in the same range than the healthy participants rating (SYNCH1PP-ASYNCH3PP: mean = 0.12, sd ± = 0.23, p < .001; ASYNCH1PP-ASYNCH3PP:mean = 0.12, sd ± = 0.21, p = 0.314) which suggest that we were able to apply the same manipulation performed on the healthy participants with the patient. We did not find any significant difference between ASYNCH1PP and ASYNCH3PP compared to the healthy population (ASYNCH1PP-ASYNCH3PP: mean = -3.68e-03, sd ± = 0.10, p = 0.21).

Figure
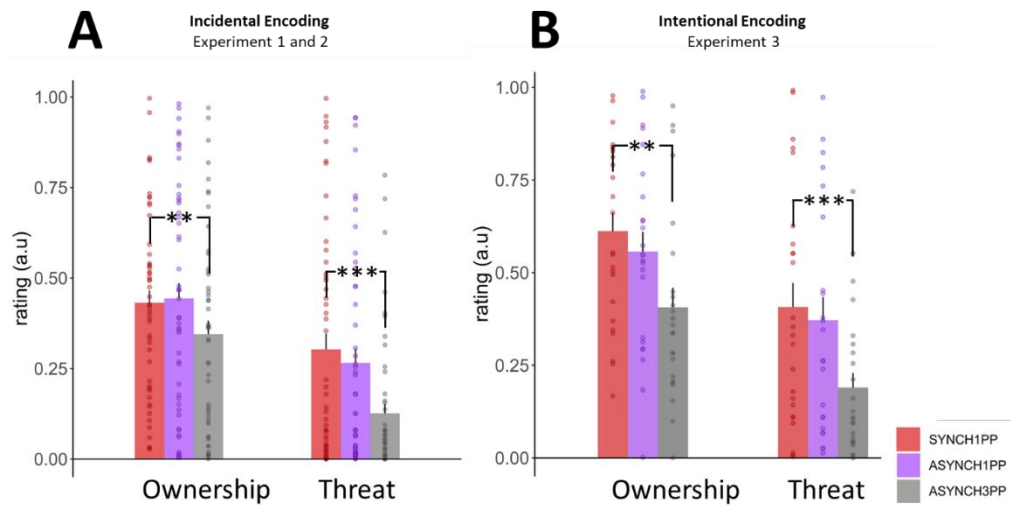
Supplementary Figure 1: BSC ratings during encoding of scenes under different visuomotor conditions. A. Incidental measure of ownership (Experiments 1 and 2). Participants had a higher ownership and were more afraid of the under visuomotor and perspectival congruency (SYNCH1PP, red) compared to visuomotor and perspectival mismatch (ASYNCH3PP, grey), no difference was observed between visuomotor and perspectival congruency (SYNCH1PP) and visuomotor mismatch (ASYNCH1PP, purple). ** indicates significance level with p-value <0.01 as tested with a linear mixed model N = 50. **B. Intentional measure of ownership (Experiments 3).** Participant had a higher ownership and were more afraid of the threat under visuomotor and perspectival congruency (SYNCH1PP, red) compared to visuomotor and perspectival mismatch (ASYNCH3PP, grey), no difference was observed between visuomotor and perspectival congruency (SYNCH1PP) and visuomotor mismatch (ASYNCH1PP, purple). ** indicates significance level with p-value <0.01 as tested with a linear mixed model N = 25.
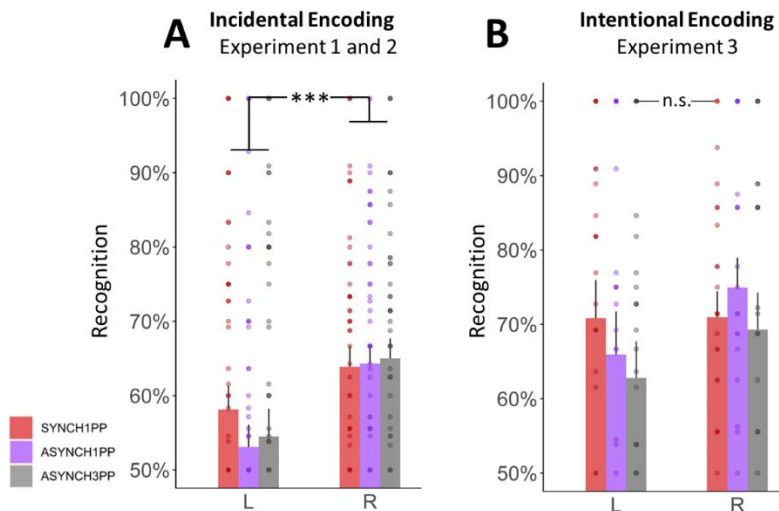
Supplementary Figure 2: Effect of objects changes laterality on recognition. A. Effect of the side of the object change under incidental encoding instruction (Experiment 1 and 2). There was a significant main effect of object side but no interaction between conditions and object side under the incidental encoding instruction as tested with linear mixed model, N = 50. *** indicates significance level with p-value <0.001. **B. Effect of the side of the object change under intentional encoding instruction (Experiment 3).** There was no effect of object laterality under intentional encoding instruction. linear mixed model, N = 25.

Date of diagnosis
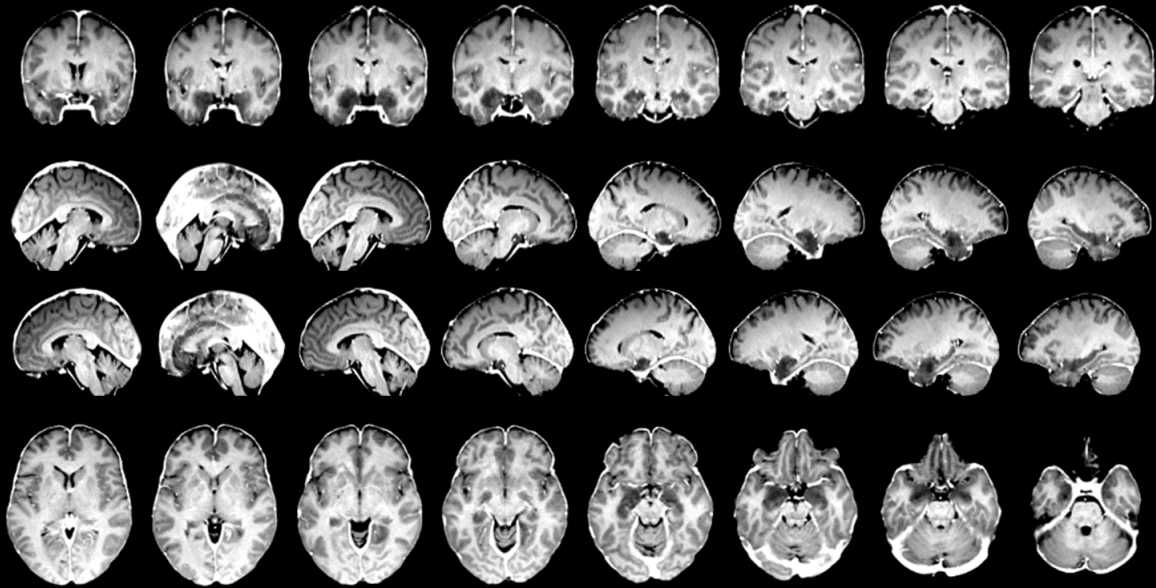
8 months after diagnosis
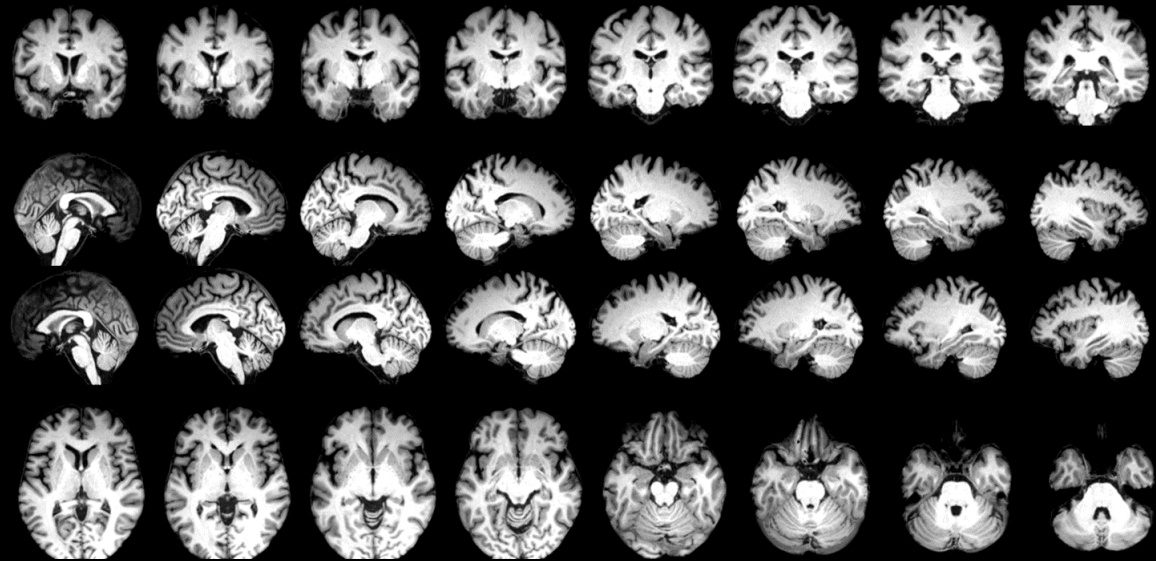
Supplementary Figure 3: Patient's lesion on the day of the diagnosis and eight month later. Anatomical scan of the patient on the day of the diagnosis (top panel) acquired with a Siemens MR-scanner (3T). dark regions around the left hippocampus show sign of inflammation. Anatomical scan of the patient taken eight month after the diagnosis (lower panel). Clear amelioration of the inflammation around the hippocampal regions although the patient did not recover from her amnestic deficit.

Table

Higher SoA in conditions without visuomotor manipulation under incidental encoding instruction

	Estimate	t-value	p-value
(Intercept)	0.654	12.383	<0.001 ***
factor(Conditions)ASYNCH1PP	-0.067	-2.931	0.003**
factor(Conditions)ASYNCH3PP	-0.065	-2.841	0.005**
factor(XP)MRI	-0.045	-0.652	0.515

Table 1: Incidental Encoding Agency: *Agency ~ Conditions + XP + random(Participants).*

	Estimate	t-value	p-value
(Intercept)	0.464	8.285	<0.001 ***
factor(Conditions)ASYNCH1PP	0.012	0.387	0.699
factor(Conditions)ASYNCH3PP	-0.087	-2.903	0.004 **
factor(XP)MRI	-0.833	-0.833	0.405

Table 2: **Incidental Encoding Ownership:** *Ownership ~ Conditions + XP +random(Participants).*

	Estimate	t-value	p-value
(Intercept)	0.289	5.557	<0.001 ***
factor(Conditions)ASYNCH1PP	-0.037	-0.936	0.349
factor(Conditions)ASYNCH3PP	-0.176	-4.451	<0.001 ***
factor(XP)MRI	0.024	0.384	0.701

Table 3: Incidental Encoding Threat: *Threat ~ Conditions + XP + random(Participants).*

	Estimate	t-value	p-value
(Intercept)	0.068	2.678	0.007 **
factor(Conditions)ASYNCH1PP	0.012	0.942	0.346
factor(Conditions)ASYNCH3PP	-0.013	-1.043	0.297
factor(XP)MRI	0.061	1.829	0.067

Table 4*: Incidental Encoding Control: Control ~ Conditions + XP + random(Participants).*

	Estimate	z-value	p-value
(Intercept)	0.643	6.925	<0.001 ***
factor(Conditions)ASYNCH1PP	0.025	0.355	0.723
factor(Conditions)ASYNCH3PP	0.064	0.929	0.353
factor(Environment)ENV2	0.207	2.969	0.003 **
factor(Environment)ENV3	-0.002	-0.031	0.975
factor(XP)MRI	-0.025	-0.243	0.808

Table 5: Incidental Encoding Performance: *Performance ~ Conditions + Scene + XP + random(Participants).*

	Estimate	z-value	p-value
(Intercept)	0.212	1.348	0.178
factor(Conditions)ASYNCH1PP	-0.201	-1.421	0.155
factor(Conditions)ASYNCH3PP	-0.177	-1.238	0.216
Factor(Laterality) R	0.288	2.028	0.043 *
factor(Environment)ENV2	0.645	6.440	<0.001 ***
factor(Environment)ENV3	0.091	0.917	0.359
factor(XP)MRI	-0.277	-1.946	0.052
factor(Conditions)ASYNCH1PP × factor(Laterality)R	0.145	0.737	0.461
factor(Conditions)ASYNCH3PP × factor(Laterality)R	0.162	0.820	0.412

Table 6: **Incidental Encoding effect of object laterality:***Performance ~ Conditions*ObjectLaterality(L/R) + Scene + XP + random(Participants).*

	Estimate	t-value	p-value
(Intercept)	0.695	13.684	<0.001 ***
factor(Conditions)ASYNCH1PP	-0.042	-1.202	0.229
factor(Conditions)ASYNCH3PP	-0.111	-3.159	0.002 **

Table 7: Intentional Encoding Agency: *Agency ~ Conditions + random(Participants).*

	Estimate	t-value	p-value
(Intercept)	0.612	11.760	<0.001 ***
factor(Conditions)ASYNCH1PP	-0.055	-1.226	0.220
factor(Conditions)ASYNCH3PP	-0.206	-4.590	<0.001 ***

Table 8: Intentional Encoding Ownsership: *Ownership ~ Conditions + random(Participants).*

	Estimate	t-value	p-value
(Intercept)	0.407	7.136	<0.001 ***
factor(Conditions)ASYNCH1PP	-0.035	-0.508	0.612
factor(Conditions)ASYNCH3PP	-0.217	-3.126	0.002 **

Table 9: Intentional Encoding Threat: *Threat ~ Conditions + random(Participants).*

	Estimate	t-value	p-value
(Intercept)	0.179	5.600	<0.001 ***
factor(Conditions)ASYNCH1PP	-0.010	-0.557	0.578
factor(Conditions)ASYNCH3PP	-0.028	-1.503	0.133

Table 10: Intentional Encoding Control: *Control ~ Conditions + random(Participants).*

	Estimate	z-value	p-value
(Intercept)	1.211	8.607	<0.001 ***
factor(Conditions)ASYNCH1PP	-0.328	-3.058	0.002 **
factor(Conditions)ASYNCH3PP	-0.316	-2.949	0.003 **
factor(Environment)ENV2	0.013	0.119	0.905
factor(Environment)ENV3	0.100	0.943	0.346

Table 11: *Performance ~ Conditions + Scene + random(Participants).*

	Estimate	z-value	p-value
(Intercept)	0.671	3.087	0.002 **
factor(Conditions)ASYNCH1PP	-0.399	-1.87	0.062
factor(Conditions)ASYNCH3PP	-0.398	-1.864	0.062
Factor(Laterality) R	0.037	0.168	0.867
factor(Environment)ENV2	0.5	283	0.001 **
factor(Environment)ENV3	0.255	1.662	0.095
factor(Conditions)ASYNCH1PP × factor(Laterality)R	0.502	0.737	0.097
factor(Conditions)ASYNCH3PP × factor(Laterality)R	0.194	0.650	0.515

Table 12: *Performance ~ Conditions*ObjectLaterality(L/R) + Scene + random(Participants).*

	Estimate	t-value	p-value
(Intercept)	0.039	1.700	0.089
factor(Conditions)ASYNCH1PP	-0.045	-2.570	0.010
factor(Conditions)ASYNCH3PP	-0.045	-2.596	0.009 **
factor(Environment)ENV2	-0.012	-0.668	0.504
factor(Environment)ENV3	-0.006	-0.323	0.747

Table 13: Hippocampal ERS Success ~ Conditions + Scene + random(Participants).

	Estimate	t-value	p-value
(Intercept)	0.039	2.254	0.024 *
factor(Conditions)ASYNCH1PP	-0.010	-0.478	0.633
factor(Conditions)ASYNCH3PP	-0.033	-1.628	0.103
factor(Environment)ENV2	-0.009	-0.462	0.644
factor(Environment)ENV3	-0.002	-0.120	0.904

Table 14: Orbito-frontal ERS Success ~ Conditions + Scene + random(Participants).

	Estimate	t-value	p-value
(Intercept)	0.008	0.327	0.743
factor(Conditions)ASYNCH1PP	-0.048	-2.769	0.006 **
factor(Conditions)ASYNCH3PP	-0.011	-0.637	0.524
factor(Environment)ENV2	0.033	1.910	0.056
factor(Environment)ENV3	0.001	0.083	0.934

Table 15: Middle temporal gyrus ERS Success ~ Conditions + Scene + random(Participants).

	Estimate	t-value	p-value
(Intercept)	0.061	1.795	0.073
factor(Conditions)ASYNCH1PP	-0.001	-0.043	0.966
factor(Conditions)ASYNCH3PP	-0.030	-1.590	0.112
factor(Environment)ENV2	0.003	0.155	0.877
factor(Environment)ENV3	-0.029	-1.544	0.123

Table 16: *Calcarine ERS Success ~ Conditions + Scene + random(Participants).*

Model 0 : *Performance ~ ERS Hippocampus + Scene + random(Participants)*

Model1: *Performance ~ ERS Hippocampus * Conditions + Scene + random(Participants)*

	AIC	BIC	logLik	deviance	Chisq	Df	Pr(>Chisq)
Model 0	159.731	146.071	85.86549	171.731			
Model 1	159.834	137.068	89.91708	179.834	8.103189	4	0.087871

Table 17 : Model comparison : *performance explained by ERS Hippocampus with or without conditions.*

	Estimate	t-value	p-value
(Intercept)	0.661	40.842	<0.001***
ERS	0.291	2.723	0.006 **
factor(Environment)ENV2	0.052	2.748	0.006 **
factor(Environment)ENV3	-0.008	-0.409	0.682

Table 18: *Performance ~ Hippocampal ERS + Scene + random(Participants).*

	[x y z]	k	p-value
Cluster	[6 -2 54]	856	0.02

Table 19:*Synch1pp-(Asynch1PP+Asynch3PP) BSC session.*

	Estimate	t-value	p-value
(Intercept)	0.661	40.842	<0.001***
ERS	0.291	2.723	0.006 **
factor(Environment)ENV2	0.052	2.748	0.006 **
factor(Environment)ENV3	-0.008	-0.409	0.682

Table 20: *Performance ~ Middle temporal gyrus ERS + Scene + random(Participants).*

	Estimate	t-value	p-value
(Intercept)	0.019	0.877	0.380
factor(Conditions)ASYNCH1PP	-0.013	-1.147	0.252
factor(Conditions)ASYNCH3PP	-0.008	-0.714	0.475
ERS	0.199	7.404	<0.001***
Trials	-0.002	-4.674	<0.001***
factor(Conditions)ASYNCH1PP × ERS	-0.192	-5.264	<0.001***
factor(Conditions)ASYNCH3PP × ERS	-0.069	-1.896	0.058

Table 21:*Hippocampal ERS ~ Premotor ERS *Conditions +Trials + random(Participants).*

	Estimate	t-value	p-value
(Intercept)	0.035	1.269	0.205
ERS	0.194	6.765	<0.001***
Trials	-0.003	-3.730	<0.001***

Table 22: SYNCH1PP: Hippocampal ERS ~ Premotor ERS *Conditions +Trials + random(Participants).

	Estimate	t-value	p-value
(Intercept)	0.001	0.045	0.964
ERS	-0.038	-1.366	0.172
Trials	-0.002	-2.254	0.024 *

Table 23: ASYNCH1PP: Hippocampal ERS ~ Premotor ERS *Conditions +Trials + random(Participants).

	Estimate	t-value	p-value
(Intercept)	0.012	0.564	0.573
factor(Conditions)ASYNCH1PP	-0.019	-1.692	0.091
factor(Conditions)ASYNCH3PP	-0.012	2.454	0.262
ERS	0.061	7.404	0.014
Trials	-0.001	-2.961	0.003 **
factor(Conditions)ASYNCH1PP × ERS	0.007	0.216	0.829
factor(Conditions)ASYNCH3PP × ERS	0.006	0.171	0.864

Table 24: Hippocampal ERS ~ Left SMA ERS *Conditions +Trials + random(Participants).

	Estimate	t-value	p-value
(Intercept)	0.020	0.946	0.344
factor(Conditions)ASYNCH1PP	-0.019	-1.674	0.094
factor(Conditions)ASYNCH3PP	-0.012	-1.106	0.269
ERS	0.006	0.260	0.795
Trials	-0.002	-3.962	<0.001***
factor(Conditions)ASYNCH1PP × ERS	-0.002	-0.059	0.953
factor(Conditions)ASYNCH3PP × ERS	0.046	1.366	0.172

Table 25: Hippocampal ERS ~ Right SMA ERS *Conditions +Trials + random(Participants).

Model 0: Performance (binomial) ~hippocampal ERS * Conditions + Trials +random(Participants)

Model 1: Performance (binomial) ~hippocampal ERS * Conditions *Stimulus+ Trials +random(Participants)

	AIC	BIC	logLik	deviance	Chisq	Df	Pr(>Chisq)
Model 0	3580.075	3627.8	1782.04	3564.075			
Model 1	3416.513	3500.031	1694.26	3388.513	175.5622	6	<0.001

Table 26: Model comparison : performance (trial-by-trial) explained by hippocampal ERS and conditions or hippocampal ERS, conditions, and stimulus type.

	Estimate	z-value	p-value
(Intercept)	-0.368	-2.910	<0.001***
factor(Conditions)ASYNCH1PP	0.088	0.661	0.509
factor(Conditions)ASYNCH3PP	0.104	0.780	0.435
ERS	-0.411	-1.168	0.243
Factor(Stimulus)NoChange	1.009	6.874	<0.001***
Trials	0.028	7.684	0.001 **
factor(Conditions)ASYNCH1PP × ERS	0.650	1.293	0.196
factor(Conditions)ASYNCH3PP × ERS	0.684	1.342	0.180
factor(Conditions)ASYNCH1PP × Stimulus(NoChange)	0.168	0.791	0.429
factor(Conditions)ASYNCH3PP × Stimulus(NoChange)	0.056	3.524	0.787
ERS x factor(Stimulus) NoChange	1.862	3.524	<0.001***
factor(Conditions)ASYNCH1PP × ERSx factor(Stimulus) NoChange	-1.073	-1.380	0.168
factor(Conditions)ASYNCH3PP × ERSx factor(Stimulus) NoChange	-2.043	-2.604	0.009 **

***Table 27**: Performance ~ Hippocampal ERS Conditions*Stim +Trials + random(Participants).*

	Estimate	z-value	p-value
(Intercept)	-0.105	-0.686	0.493
factor(Conditions)ASYNCH1PP	0.089	0.670	0.503
factor(Conditions)ASYNCH3PP	0.112	0.835	0.403
ERS	-0.509	-1.429	0.153
Trials	0.028	7.684	0.001 **
factor(Conditions)ASYNCH1PP × ERS	0.725	1.435	0.151
factor(Conditions)ASYNCH3PP × ERS	0.777	1.516	0.130

Table 28: *Performance (Change) ~ Hippocampal ERS *Conditions +Trials + random(Participants).*

	Estimate	z-value	p-value
(Intercept)	0.324	1.487	0.137
factor(Conditions)ASYNCH1PP	0.276	1.587	0.112
factor(Conditions)ASYNCH3PP	0.180	1.065	0.287
ERS	1.545	3.527	<0.001***
Trials	0.052	8.290	<0.001***
factor(Conditions)ASYNCH1PP × ERS	-0.593	-0.916	0.360
factor(Conditions)ASYNCH3PP × ERS	-1.665	-2.551	0.011 *

Table 29: *Performance (NoChange) ~ Hippocampal ERS *Conditions +Trials + random(Participants).*

	Estimate	z-value	p-value
(Intercept)	-0.013	-0.042	0.966
ERS	1.720	3.520	<0.001***
Trials	0.075	6.260	<0.001***

Table 30: *Performance (No Change) ~ Hippocampal ERS SYNCH1PP +Trials + random(Participants).*

	Estimate	z-value	p-value
(Intercept)	0.742	2.512	0.012 *
ERS	-0.223	-0.429	0.668
Trials	0.043	4.036	<0.001***

Table 31: *Performance (No Change) ~ Hippocampal ERS ASYNCH3PP +Trials + random(Participants).*

Statement	Scale	Reference
My memory for this event involves sound	1-7 little/A lot	MCQ
My memory for this event involves smell	1-7 little/A lot	MCQ
My memory for this event involves touch	1-7 little/A lot	MCQ
The overall tone of the memory is	Negative/Neutral/Positive	MCQ
In this event I was	An observer /A participant	MCQ
I remember the event through my own eyes as during the event	1-7 Not at all/Definitely	MCQ
When you picture this event do you visualize it as a continuous video that plays with break, moving video clips with some breaks, one moving image or is it more like a set of snapshot with no movement, or something else?	1-7 One smooth video/video clips with breaks/one moving image/snapshot in sequence/one static snapshot/Hazy image/no image	EAMI
How often would you estimate you have thought about this memory since it first occurred?	1- 4 Frequently/Occasionnaly/Rarely/Never Never/Rarely/Occasionnaly/Frequently	EAMI
How often would you estimate you have spoken about this memory since it first occurred?	1-4 Frequently/Occasionnaly/Rarely/Never Never/Rarely/Occasionnaly/Frequently	EAMI
When you recall this event are you viewing the scene through your « own eyes » or can you see yourself in the memory from a third-person perspective?	Own eyes/Mixture/Third person/something different/no imagery	EAMI
When you recall this event how would you describe it in terms of vividness? This can apply to the richness of sights, sounds, smells, tastes, touch, and any movements you may have made.	1-7 very vivid/very vague 1-7 very vague/very vivid	EAMI
The relative spatial arrangement of people in my memory for the event is	1-7 Vague/Distinct	MCQ
My memory for the time when the event takes place is	1-7 Vague/Distinct	MCQ
When I remember the event, I see myself entirely in the scene as if I was watching a movie	1-7 Not at all/Definitely	MCQ
When I think about or tell this memory, I feel like I relive it as it happened	1-7 Not at all/Definitely	MCQ

I remember the movements and gestures I made with my body at the time of the event	1-7 / Vague/Distinct	In-house
My memory for this event is	1-7 Dim/Clear	MCQ
My memory for this event involves visual details	1-7 Little/ A lot	MCQ
My memory for this event is	1-7 Sketchy/very detailed	MCQ
My memory for the location where the event takes place is	1-7 Vague/Distinct	MCQ
Relative spatial arrangement of objects in my memory for the event is	1-7 Vague/Distinct	MCQ
When you think about this event now, do you re-experience any of the emotion you originally felt at the time? To what extent are you re-experiencing this emotion as a percentage?	0/25/50/75/100%	EAMI
To what extent are you re-experiencing this memory as a percentage?	0/25/50/75/100%	EAMI
Would you say you are reliving this memory or looking back on it?	Reliving/Looking back	EAMI
I remember how I felt at the time when the event took place	1-7 Not at all/Definitely	MCQ
I remember what I thought at the time	1-7 Not at all/Definitely	MCQ

Table 32: *Autonoetic consciousness questionnaire. Scale from original questionnaire is indicated in black, new scale is indicated in green.*

3. Study 2: Autonoetic consciousness depends on sense of agency and sensorimotor context at encoding

Authors

Nathalie Heidi Meyer[1], Baptiste Gauthier[2], Jevita Potheegadoo[1], Juliette Boscheron[1], Elizabeth Franc[1], Florian Lance[1], Olaf Blanke[,1,3]

Affiliations

[1] Laboratory of Cognitive Neuroscience, Neuro-X Institute & Brain Mind Institute and Center for Neuroprosthetics, Faculty of Life Sciences, Ecole Polytechnique Fédérale de Lausanne, Geneva, Switzerland

[2] Clinical Research Unit, Neuchâtel Hospital Network, 2000 Neuchâtel, Switzerland

[3] Department of Clinical Neurosciences, University Hospital Geneva, Rue Micheli-du-Crest 24, 1205, Geneva Switzerland

3.1 Abstract

Autonoetic consciousness (ANC), the ability to re-experience a personal past event has been theoritized to link episodic memory and self-consciousness in the act of remembering. Although the sensory aspect and the self-consciousness component of ANC have been investigated separately, multiple pieces of evidence point towards an association of self-consciousness and sensory information as important modulators of ANC. Bodily self-consciousness (BSC), defined as a unitary sense of self within the body boundary arising from the multisensory and sensorimotor integration of bodily signals, can be conceived as the missing link joining sensorimotor context, self-consciousness, and ANC together. Recently, immersive virtual reality (VR) enabled researchers to collect empirical evidence on the effect of BSC on ANC. However, how BSC and its related subjective experience at encoding affect ANC remains unknown. In this study, we induced a sensorimotor manipulation to modulate the sense of agency (SoA) of participants during the encoding of virtual scenes while simultaneously recording brain activity using fMRI. We found that ANC tested one week later was dependent on the SoA experienced during encoding only under the condition of successful sensorimotor integration. This change was conveyed by the insula and its functional connectivity with apriori chosen BSC-related and memory-related regions of interest. Together, our results demonstrate that ANC depends on SoA and the sensorimotor aspects of BSC. This seems to be mediated at the neural level by the insula, which functional connectivity enhances the experience associated with its remembering.

3.2 Introduction

Autonoetic consciousness (ANC) is a defining feature of episodic memory which enable one to mentally travel back in time and re-experience the subjective characteristics of an event personally experienced in the past. Introduced by Tulving (Tulving, 1985; M. A. Wheeler et al., 1997), the notion of ANC revolves around the recollection of sensory and subjective experience during a past event. Conceptually, ANC is often related at the crossroad between self-consciousness and memory as it relies simultaneously on memory processes and the ability to project oneself in the past.

In the aim to provide clinical evidence linking self-consciousness and ANC, Klein specified the necessary features of self-consciousness for ANC. In a series of papers, he proposed that ANC could rise from the joint association of sense of ownership (SoO, the feeling that the body belongs to oneself), sense of agency (SoA, the feeling of being in control of the body and its related movements), self-reflection and personal temporality (S. Klein, 2013; S. B. Klein et al., 2011; S. B. Klein & Nichols, 2012). Although his work provides convincing clinical evidence to link ANC and self-consciousness, it does not focus on the sensory aspects common to ANC retrieval and self-consciousness.

However, sensory information is at the roots of both ANC and self-consciousness: the definition of ANC itself implies a recollection of sensory experience for events encoded personally in the past. Moreover, one of the minimal forms of self-consciousness, called bodily self-consciousness (BSC), arises from the multisensory and sensorimotor integration of external stimuli, which creates the experience of a unitary self within the body boundaries. Interestingly, SoO and SoA, along with the first-person perspective (1PP) are part of the main subcomponent of BSC (Blanke, 2012; Blanke et al., 2015; Blanke & Metzinger, 2009; Lenggenhager et al., 2014). The study of BSC relies mainly on the experimental manipulation of multisensory or sensorimotor signals and its induction of mismatch to create bodily illusions. For instance, in the case of the full-body illusion (FBI), participants' self-location is shifted toward a virtual mannequin observed in virtual reality (VR) when the back on the mannequin is stroked synchronously with participants' back (Lenggenhager et al., 2007). The extended use of VR in the field of cognitive neurosciences made it possible to experimentally manipulate SoO using visuotactile (Hoover & Harris, 2016; Kalckert & Ehrsson, 2014) and perspectival (Freude et al., 2020) mismatch and SoA using mainly visuomotor mismatch (Jeunet et al., 2018; Kalckert & Ehrsson, 2012).

Linking BSC and Klein's work, one can consider BSC as the junction between ANC and self-consciousness processes. The multisensory and sensorimotor integration of bodily signals in the present (i.e., at encoding) provides the necessary components for the creation of a subjective and personal experience, later retrieved during ANC processes. This link is further supported by several brain regions shared by both ANC and BSC reported in the literature such as precuneus (Freton et al., 2014; Trimble & Cavanna, 2008), medial prefrontal cortex (mPFC;

Epstein et al., 2002; Gusnard et al., 2001; Keenan et al., 2000), angular gyrus (Bonnici et al., 2018; Bréchet et al., 2018; Ramanan et al., 2018), and insula (Heydrich & Blanke, 2013; Ronchi et al., 2015; Xie et al., 2012). Yet, only a few studies have shown that a stronger ANC was associated with successful multisensory and sensorimotor integration and, therefore, BSC. Hence, a change from a naturalistic first-person perspective (1PP) to a third-person perspective (3PP) at encoding decreased the vividness of a memory and was related to hippocampal activity at retrieval (Bergouignan et al., 2014). Similarly, a disruption of SoO using visuotactile mismatch was shown to decrease the emotional and global reliving of an event (Iriye & Ehrsson, 2022). Recently, our group has shown that a change from naturalistic 1PP to an absence of body view at encoding impacted the peri-encoding resting state connectivity of the right parahippocampus with the hippocampus, suggesting that the multisensory and sensorimotor integration of bodily signals modulates encoding processes. However, these studies did not link the strength of the subjective experience generated by BSC at encoding with the strength of the recollection, as most of them did not measure the subjective experience related to the BSC manipulation.

To answer this question, we investigated how BSC and its related subjective experience at encoding would affect ANC, at the behavioral and neural levels. We used immersive VR to manipulate BSC during the encoding of virtual scenes and measured ANC one week later. We investigated how the subjective experience related to BSC (SoA) at encoding was linked with ANC, and how this was mediated at the neural level by the functional connectivity at encoding of BSC and memory-related brain regions. We predicted that ANC strength would increase as a function of SoA. At the neural level, we predicted functional connectivity changes between the level of BSC manipulation and that this change would predict ANC strength.

3.3 Methods

Participants included in this study are the same participants than the one described in Study 1 (Meyer & Gauthier, in prep). We recruited 26 participants (7 male; mean age 23 ± 3.4 years) in Experiment 1, 29 participants (11 male, 3 gender-nonconforming, mean age 24 ± 3.4 years) in Experiment 2, and 27 participants (10 male, mean age 27 ± 3.5) in Experiment 3. All participants were right-handed (Flinders Handedness Survey; FLANDERS, Grimshaw, 2013) and reported no history of neurological or psychiatric disorder and no drug consumption in the 48h hours preceding the experiment. Participants provided written informed consent following the local ethical committee (Cantonal Ethical Committee of Geneva: 2015-00092, and Vaud and Valais: 2016-02541), the declaration of Helsinki (2013), and were financially compensated for their participation.

Material and technical setup

In Experiments 1 and 3, participants were lying down in a mock Magnetic Resonance (MR) scanner wearing a head-mounted display (HMD; Oculus Rifts S, refreshing rate 80Hz, resolution 1280 x 1440 per eye, 660 ppi) and holding custom response devices in their hands (two hand-held tennis balls with integrated buttons and reflective 6-degree-of-freedom motion trackers) to simultaneously record participants' answers and track participants arm movement using three motion tracking cameras (Qualisys Oqus 500+m cameras with 180 Hz, 4 MegaPixel resolution). Experiment 2 was similar but participants were lying in an MR scanner, therefore they were wearing MRI-compatible goggles allowing stereoscopic rendering at 60 Hz with a diagonal field of view of 60° (Visual System HD, NordicNeuroLab, Bergen, Norway) similar as (Gauthier et al., 2021). Instead of three motion-tracking cameras, the MR scanner contained 6 motion-tracking cameras to track participants' body movements.

The experiments consisted of three sessions: An incidental encoding session, a recognition task one hour after the encoding, and an ANC questionnaire assessed by phone one week after the encoding. For the scope of this paper, we will not discuss the results of the recognition task and will focus on the ANC assessment.

Encoding session

The encoding session was similar to the one used in (Meyer and Gauthier, in prep). Participants were instructed to move their right arm between two virtual black spheres, while observing an avatar during the encoding of three indoor virtual scenes containing 18 objects each. Each scene was presented for 30 seconds and associated with a specific modulation of visuomotor and perspectival congruency: no modulation (SYNCH1PP, preserved BSC), where participants observed the avatar at the first-person perspective with the avatar arm moving synchronously with respect to participants' movement; visuomotor incongruency (ASYNCH1PP, light manipulation of BSC), where participants observed the avatar at the first-person perspective but the movement were asynchronous (fluctuating delay between 800-

1000s) and visuomotor and perspectival incongruency, in which additionally to the asynchrony, the avatar was shifted in front of participant's view at the third person perspective (ASYNCH3PP, strong manipulation of BSC). The association between the scene and the conditions were pseudorandomized between participants. Each scene was presented four times for each experimental condition with an inter-trial of five seconds to avoid potential carry-over effects from one condition to another. To ensure that the movement of the arm was well performed and decreased the novelty effect of the scene presentation, participants did a familiarization before the encoding (See Supplementary text).

BSC assessment

Immediately after the encoding, participants were presented with a fourth outdoor scene in which we assessed the subjective experience (SoA and SoO) related to the BSC state. They were given the same instruction as during the encoding session and observed an avatar in SYNCH1PP, ASYNCH1PP, and ASYNCH3PP (each presented twice for 30 seconds, with a randomized order). Participants had to rate on a continuous scale, five statements to assess their SoA ("I felt that I was controlling the virtual body"), SoO ("I felt that the virtual body was mine"), response to a threat ("I was afraid to be hurt by the knife"), and experimental bias("I felt that I had more than three bodies" and "I felt that the trees were my body").

Autonoetic consciousness assessment

One week after the encoding, participants were called back to assess their ANC for each event encoded in VR. For each scene encoded (and therefore each condition), participants were asked to answer a series of questions taken from the "memory characteristic questionnaire" (MCQ, Johnson et al., 1988), the "episodic autobiographical memory interview" (EAMI part B, (Irish, 2008; Irish et al., 2011) and the "affected limb intentional feeling questionnaire" (ALEFq; Crema et al., 2022). **Table 1** describes all the items included in the questionnaire. The participants were told to remember the first part of the experiment (referred as the part before the break), and were cued with the name of the scene ("living room", "cabin" and "changing room"). They were asked to briefly describe the scene before answering the questionnaire to make sure that the questions would capture the specific condition associated with the remembered scene.

Behavioral data analysis

Behavioral analysis was applied using R (R Core Team, 2022) and R studio (RStudio, 2022). Linear mixed models were computed using the package *lme4* (Walker et al., 2015) and *lmerTest* (Christhenssen RHB et al., 2017).

Bodily self-consciousness

To quantify how the encoding manipulation impacted the SoA, we used a linear mixed model with the SoA ratings as dependent variable, the conditions as fixed factor with three levels (SYNCH1PP, ASYNCH1PP, and ASYNCH3PP), and participants as random factor. We applied the

same model to explain SoO, the response to threat and the experimental bias (computed as the mean between the two control questions).

Autonoetic consciousness dimension reduction

We first reversed the scale of three questions extracted from the EAMI questionnaire (Q1: " How often would you estimate you have thought about this memory since it first occurred"; Q2: " How often would you estimate you have spoken about this memory since it first occurred? "; Q3: "When you recall this event how would you describe it in terms of vividness? This can apply to the richness of sights, sounds, smells, tastes, touch, and any movements you may have made.") to have higher ratings corresponding to stronger recollection (the original EAMI questionnaire associate the lowest ratings, 1, as strong vividness and 7 a slow vividness for example). Original scaling is depicted in black in Table 1, and reversed scaling in green.

To identify which questions captured at best the difference of ANC questionnaire between conditions, we used a kmeans clusterization (package *ggpubr* (Kassambara, 2020) and *factoextra* (Mundt F, 2020) applied on the difference of normalized ANC ratings between manipulated and non-manipulated BSC conditions (SYNCH1PP – (ASYNCH1PP + ASYNCH3PP). We used a maximum iterations of 10000. We used 6 clusters as determined using the Elbow method (Nalwade et al., 2013), using the package *nFactors* in R studio (Magis D, 2020). We then separated the items of the questionnaires accordingly.

Autonoetic consciousness and sense of agency

To quantify the difference of ANC between conditions, we computed an ANC score for each participant and each condition, by suming the normalized ratings of the questionnaire together, to obtain one score per participant per condition. To investigate the relationship between ANC and SoA, the main BSC manipulation, we compared two linear mixed model: the first explained the ANC score (dependent variable) with the conditions (model 0) the second explained ANC score (dependent variable) with the conditions and interaction with the SoA score (model 1). For each model, the experiment was added as a covariate (fixed factor with three levels) and the participants were added as random factor. We selected the model with the lowest AIC and which passed the X_2 test. We then applied the same model on the subfactor to verify if each factor individually could capture the same effect as the model with the overall ANC score.

MRI acquisition

MR images were acquired using a 3T MRI scanner (MAGNETOM PRISMA; Siemens) using a 64-channel head coil at Campus Biotech Geneva. Each participant from Experiment 2 underwent a 5 min anatomical imaging using a T1-weighted MPRAGE sequence (TR = 2300 ms, TE = 2.25 ms, TI = 900 ms, Slice thickness = 1 mm, In-plane resolution = 1 mm × 1 mm, Number of slices = 208, FoV = 256 mm, Flip angle = 8). Encoding session and BSC assessment were acquired with a whole-brain T2*-weighted Echo Planar Imaging (EPI) sequence (TR = 1500 ms, TE = 30 ms, 69 slices, flip-angle = 50°, Slice thickness = 2 mm, In-plane resolution = 2 mm

× 2 mm, Multiband factor = 2, slice acquisition order = interleaved). B0 field maps were acquired to correct EPI distortion due to magnetic field inhomogeneity.

MRI preprocessing

We used the same preprocessing steps than in (Meyer and Gauthier, *in prep*). MRI data were preprocessed with SPM12 v7487 (http://www.fil.ion.ucl.ac.uk/spm). We computed voxel displacement maps for the first and second sessions for each subject using pre-subtracted Phase and Magnitude Images (Short and Long echo times = 4.92 and 7.38 ms respectively, Blip direction = -1, total EPI readout time = 34.72 ms). Functional images were realigned to the first image of each session and unwarped using the voxel displacement maps with standard parameters. We applied a slice timing correction to correct for time delay due to volume acquisition time. Anatomical images were segmented using the unified segmentation approach (Ashburner & Friston, 2005). Functional images were corrected for bias field and then coregistered with bias field-corrected segmented anatomy using normalized mutual information. Finally, coregistered functional images were normalized using the normalization parameters estimate during unified segmentation of the anatomical images.

ROI - to - ROI functional connectivity analysis

We investigated the difference of functional connectivity between conditions at encoding by performing an ROI-to-ROI analysis using the same brain regions than used in (Gauthier et al., 2020), as they are known to have high predictive power in episodic memory and BSC: bilateral hippocampus (MNI coordinates, right: 27, -21, -15; left: -26,-22,-15), parahippocampus (MNI coordinates, right: 25, -18, -26; left: -23,-19,-25), and medial prefrontal cortex (mPFC, MNI coordinates, right: 7,45,-8; left -7,51,-7) and bilateral insula (MNI coordinates, right: 35, 18, 1; left: -33,16,1). We added the angular gyrus (MNI coordinates, right: 49, -57, 35; left: -44,-64,36) and precuneus (MNI coordinates, right: 9, -57, 35; left: -6,-58, 35) because of their involvement reported in both episodic memory and BSC studies (Bonnici et al., 2016; Bréchet et al., 2018; Cabanis et al., 2013; Trimble & Cavanna, 2008). Finally, we added regions sensitive to our BSC manipulation at encoding identified using data-driven analysis described in the supplementary text: left dorsal premotor cortex (dPMC, MNI coordinates left: -19,-25, 62), and bilateral supplementary area (SMA: MNI coordinates, right: 5, -4,55; left: -4,-11,56). All ROIs were extracted using the neuromorphometrics atlas from spm (except for the data driven ROIs: SMA and dPMC). All ROIs are depicted in **Supplementary Figure 1**. We used the CONN toolbox v20.b (www.nitrc.org/projects/conn) to perform the ROI-to-ROI analysis. We first investigated whether there were functional connectivity changes between conditions (6 contrast SYNCH1PP> ASYNCH1PP, SYNCH1PP >ASYNCH3PP, SYNCH1PP > ASYNCH1PP +ASYNCH3PP, SYNCH1PP< ASYNCH1PP, SYNCH1PP < ASYNCH3PP, SYNCH1PP < ASYNCH1PP +ASYNCH3PP). We used a voxel threshold of 0.001 and an FDR cluster-size correction of 0.05.

We then extracted the functional connectivity matrixes for each participant and performed a linear mixed model in R (R Core Team, 2022, RStudio, 2022) to explain the ANC score (dependent variable) with the interaction between conditions (factor, 3 levels: SYNCH1PP, ASYNCH1PP, and ASYNCH3PP) and the functional connectivity of each node with the other regions. We used a Bonferroni correction to correct for multiple comparisons, thus the interaction terms were considered significant when the significativity threshold (p-value) was lower than 0.003 (0.05/15). We applied Pearsons' correlation separately between ANC score and each condition when there was significant interaction found in the linear mixed model.

In case a ROI node explained the ANC score of participants, we performed linear mixed model between each ROI and the significant ROI node, to further investigate with which ROI connection the ROI node was connected to explain ANC. We used a Bonferroni correction to correct for multiple comparisons. Therefore we considered a model significant when the significativity threshold (p-value) of the interaction terms was lower than 0.0035 (0.05/14). Post-hoc pairwise comparisons were applied for each condition and each ROI found significant with the ROI node.

Statement	Scale	Reference	Factor
My memory for this event involves sound	1-7 little/A lot	MCQ	Sensory reliving
My memory for this event involves smell	1-7 little/A lot	MCQ	Sensory reliving
My memory for this event involves touch	1-7 little/A lot	MCQ	Sensory reliving
The overall tone of the memory is	Negative/Neutral/Positive	MCQ	Sensory reliving
In this event I was	An observer /A participant	MCQ	Sensory reliving
I remember the event through my own eyes as during the event	1-7 Not at all/Definitely	MCQ	Sensory reliving
When you picture this event do you visualize it as a continuous video that plays with break, moving video clips with some breaks, one moving image or is it more like a set of snapshot with no movement, or something else?	1-7 One smooth video/video clips with breaks/one moving image/snapshot in sequence/one static snapshot/Hazy image/no image	EAMI	Sensory reliving
How often would you estimate you have thought about this memory since it first occurred?	1- 4 Frequently/Occasionnaly/Rarely/Never Never/Rarely/Occasionnaly/Frequently	EAMI	Sensory reliving
How often would you estimate you have spoken about this memory since it first occurred?	1-4 Frequently/Occasionnaly/Rarely/Never Never/Rarely/Occasionnaly/Frequently	EAMI	Sensory reliving
When you recall this event are you viewing the scene through your « own eyes » or can you see yourself in the memory from a third-person perspective?	Own eyes/Mixture/Third person/something different/no imagery	EAMI	Perspective and thought
When you recall this event how would you describe it in terms of vividness? This can apply to the richness of sights, sounds, smells, tastes, touch, and any movements you may have made.	1-7 very vivid/very vague 1-7 very vague/very vivid	EAMI	Perspective and thought
The relative spatial arrangement of people in my memory for the event is	1-7 Vague/Distinct	MCQ	Perspective and thought
My memory for the time when the event takes place is	1-7 Vague/Distinct	MCQ	Perspective and thought
When I remember the event, I see myself entirely in the scene as if I was watching a movie	1-7 Not at all/Definitely	MCQ	Perspective and thought

When I think about or tell this memory, I feel like I relive it as it happened	1-7 Not at all/Definitely	MCQ	Perspective and thought
I remember the movements and gestures I made with my body at the time of the event	1-7 / Vague/Distinct	In-house	Perspective and thought
My memory for this event is	1-7 Dim/Clear	MCQ	Global vividness
My memory for this event involves visual details	1-7 Little/ A lot	MCQ	Global vividness
My memory for this event is	1-7 Sketchy/very detailed	MCQ	Global vividness
My memory for the location where the event takes place is	1-7 Vague/Distinct	MCQ	Global vividness
Relative spatial arrangement of objects in my memory for the event is	1-7 Vague/Distinct	MCQ	Global vividness
When you think about this event now, do you re-experience any of the emotion you originally felt at the time? To what extent are you re-experiencing this emotion as a percentage?	0/25/50/75/100%	EAMI	Re-experience
To what extent are you re-experiencing this memory as a percentage?	0/25/50/75/100%	EAMI	Re-experience
Would you say you are reliving this memory or looking back on it?	Reliving/Looking back	EAMI	Reliving
I remember how I felt at the time when the event took place	1-7 Not at all/Definitely	MCQ	Rehearsal
I remember what I thought at the time	1-7 Not at all/Definitely	MCQ	Rehearsal

Table 1. Autonoetic consciousness (ANC) questionnaire. *Items used to assess ANC for each condition. Scale from original questionnaire is indicated in black, new scale is indicated in green.*

3.4 Results

Higher SoA under visuomotor and perspectival congruency

To verify that our SoA manipulation was successful, we compared the SoA of participants between conditions using a linear mixed model. As expected, we found that participants had a higher SoA under visuomotor and perspectival congruency (**Figure 1A**) compared to the manipulated conditions (SYNCH1PP compared to ASYNCH1PP: estimate = -0.05, t = -2.621, p = 0.01, SYNCH1PP compared to ASYNCH3PP: estimate = -0.07, t = -4.067, p <0.001). There was no effect of experiment, and we did not find any difference between conditions when applying the same linear mixed model to control questions. Therefore, the difference of SoA between conditions cannot be explained by experimental bias (See Supplementary text for the results for SoO).

Autonoetic consciousness is related to SoA under visuomotor and perspectival congruency

To investigate whether BSC and its related subjective experience (SoA) had an impact on ANC, we compared two linear mixed models to explain the ANC score of participants with the conditions (model 0) and with the interaction between conditions and SoA and selected model 1 based on the X_2 test (model 1 was significantly better than model 0, AIC_{model0} = -435.54, AIC_{model1} = -438.99, df = 3,p = 0.02). We found a significant interaction between SoA and the conditions SYNCH1PP and ASYNCH3PP (estimate = -0.13, t = -3, p = 0.003, **Figure 1B**). There was no significant interaction when comparing SYNCH1PP with ASYNCH1PP (estimate = -0.06, t = -1.5, p = 0.13). Post-hoc analysis applied separately on SYNCH1PP and ASYNCH3PP revealed a significant correlation between SoA and ANC only under visuomotor and perspectival congruency (estimate = 0.11, t = 2.25, p = 0.03). To better understand whether a change of perspective generated this interaction, we applied the same model to compare ASYNCH1PP and ASYNCH3PP (as these conditions should give rise to a comparative level of SoA, but differ in the perspective adopted) and did not find any significant interaction. Finally, to investigate whether the effect was specific to SoA or could be extended to SoO we applied the same model with SoO and did not find any significant interaction between SYNCH1PP and ASYNCH3PP (estimate = -0.05, t = -1.2, p = 0.2) nor between SYNCH1PP and ASYNCH1PP (estimate = -0.009, t = -0.23, p = 0.22). These results show that the bodily-related subjective experience at encoding impacts ANC strength.
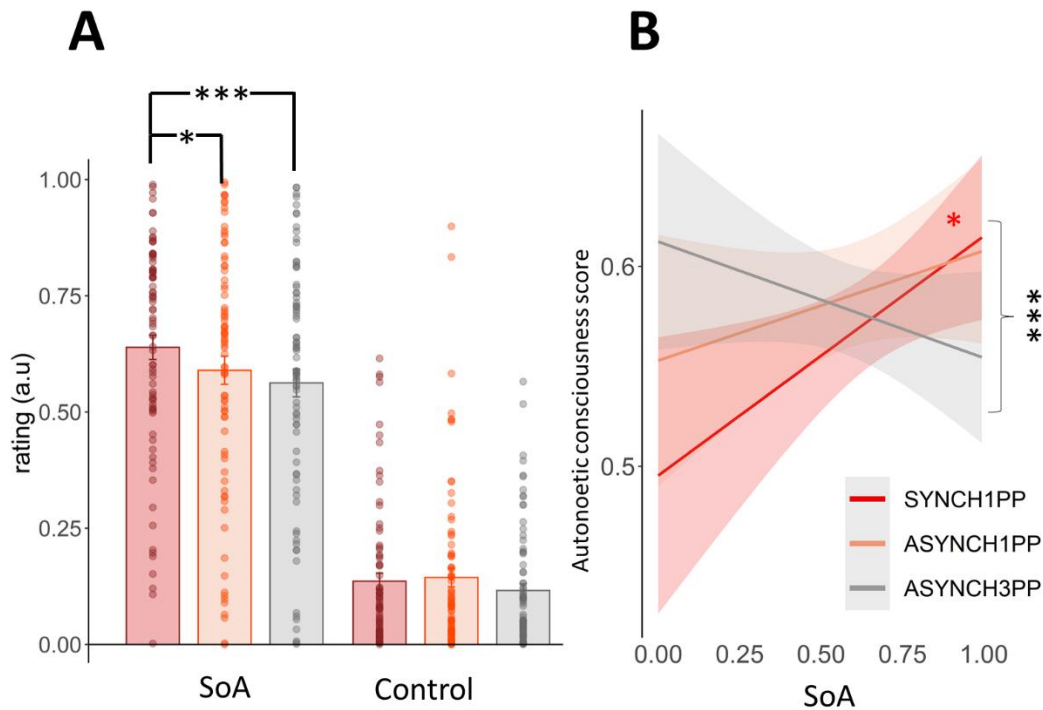
Figure 1. Autonoetic consciousness is related to SoA under visuomotor and perspectival congruency. A. Sense of agency (SoA) was higher under visuomotor and perspectival congruency (SYNCH1PP, red) compared to the two manipulated conditions (ASYNCH1PP, orange, ASYNCH3PP, grey) as tested with a linear mixed model with SoA as dependent variable and conditions as fixed factor (N = 76). B. There was a significant interaction between visuomotor and perspectival congruency (SYNCH1PP, red) and visuomotor and perspectival mismatch (ASYNCH3PP, grey) as tested with a linear mixed model, with ANC score as dependent variable, and interaction between conditions and SoA as independent variable (N = 76). SoA was positively correlated with ANC score only under visuomotor and perspectival congruency. *,*** indicates significance level with p-value <0.05 and 0.001 respectively. ANC (autonoetic consciousness) score was computed as the sum of the normalized ratings of all the ANC questionnaire items for each condition and each participant.

Global vividness and subjective re-experiencing depend on SoA under visuomotor and perspectival congruency

To investigate whether we could reduce the set of questions used for future studies, we performed a dimensionality reduction on the questionnaire items. We used an elbow method using the difference of ratings between visuomotor and perspectival congruency (SYNCH1PP) and the two manipulated conditions (ASYNCH1PP and ASYNCH3PP) and found that the questionnaire could be divided into six different factors. We then applied k-means clustering to determine how the questionnaire items would be attributed to the six factors (**Table 1**). Based on the items within a factor, we attributed a category name for each factor ("Sensory reliving", "Perspective and thoughts", "Global vividness", "Re-experience","Re-living"," Rehearsal"). We used the same model applied on the overall ANC score (model 1) for each of the six subfactors. We found that the factor using questions about the global vividness had a significant interaction between SoA and the SYNCH1PP and ASYNCH3PP conditions (estimate = -1.2, t = -2.7, p = 0.009), similar to the global score. Interestingly, the binary questions about the subjective reliving of participants ("Are you reliving the event or looking back?") was

classified as an own factor itself. Because of its content very close to the "Re-experience" factor including the emotional and global re-experiencing of participants, we regrouped the two factors together and applied a linear mixed model to the regrouped factor. Similarly to the previous results, we found a significant interaction between SoA and the questions item when comparing SYNCH1PP with ASYNCH3PP in Experiment 1 and 3 , estimate = -0.72, t = -2.8, p = 0.006). Table 2 summarizes the factor and their related questions with significant interaction between the conditions and SoA to explain ANC.

Questions	Scale	Category
My memory for this event is	1-7 Dim/Clear	Global vividness
My memory for this event involves visual details	1-7 Little/ A lot	Global vividness
My memory for this event is	1-7 Sketchy/very detailed	Global vivdness
My memory for the location where the event takes place is	1-7 Vague/Distinct	Global vividnes
Relative spatial arrangement of objects in my memory for the event is	1-7 Vague/Distinct	Global vividness
When you think about this event now, do you re-experience any of the emotion you originally felt at the time? To what extent are you re-experiencing this emotion as a percentage?	0/25/50/75/100%	Re-experience
To what extent are you re-experiencing this memory as a percentage?	0/25/50/75/100%	Re-experience
Would you say you are reliving this memory or looking back on it?	Reliving/Looking back	Reliving

Table 2. ANC factor with similar interaction than the overall ANC score. Factor and their related items with significant interaction between conditions and SoA to explain ANC.

Functional connection of the insula with memory and BSC - related areas explain ANC under visuomotor and perspectival congruency

Finally, we investigated the common neural substrate shared by ANC and BSC processes, with participants from Experiment 2, who performed the encoding session in an MR-scanner. We wanted to assess if functional connectivity between memory and BSC regions at encoding was modulated by the sensorimotor condition and could explain ANC scores measured a week later. We did not find any significant difference in the functional connectivity of the *apriori* network between conditions. Building on the behavioral results finding an interaction between the encoding conditions and SoA to explain ANC, we hypothesized that the functional connectivity between the *apriori* network (bilateral hippocampus, parahippocampus, mPFC, precuneus, angular gyrus, insula, SMA and left dPMC) should be sensitive to our SoA manipulation, hence could also interact with the encoding conditions to explain ANC. We applied a linear mixed model to explain ANC score by the interaction between the conditions and the functional connectivity of each ROI of the *apriori* network with the others.

Supplementary Table 1 summarizes the results of the interaction for each brain region. After correction for multiple comparisons using a significant threshold of 0.003 ($p_{corrected}$ = 0.05/15 = 0.003), we found a significant interaction between SYNCH1PP and ASYNCH3PP within the bilateral insula to explain ANC score (**Figure 2,** SYNCH1PP versus ASYNCH3PP, left insula: estimate = -0.06, t = -4.36, p <0.0001; right insula: estimate = -0.04, t = -3.33, p = 0.0008). The interaction between SYNCH1PP and ASYNCH1PP in the left insula was in the same direction but did not survive the correction for multiple comparisons (left insula: estimate = -0.04, t = -2.2, p = 0.028). There was also an interaction between the functional connectivity of the left insula and the two conditions encoded under visuomotor and perspectival mismatch (ASYNCH1PP versus ASYNCH3PP: estimate = -0.006, t = -3.6, p = 0.0003). Post-hoc analysis revealed a significant correlation between the functional connectivity of the insula node with ANC score only under visuomotor and perspectival congruency (SYNCH1PP, left insula: r = 0.43, t(23) = 2.3, p = 0.02; right insula: r = 0.53, t(23) = 3.05, p = 0.005; ASYNCH3PP: left insula:
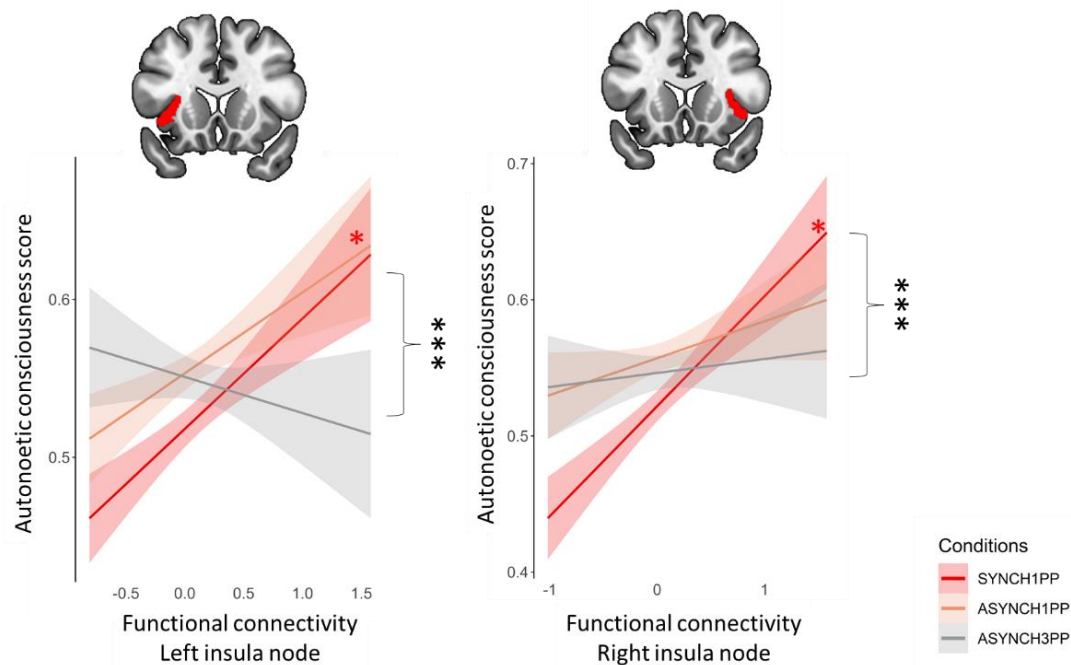
Figure 2. Functional connectivity between bilateral insula and a BSC-memory network is sensitive to SoA manipulation at encoding. *Functional connectivity of the left insula (left panel) and right insula (right panel) with the hippocampus, parahippocampus, angular gyrus, mPFC, precuneus,SMA and dPMC was positively related to ANC score under visuomotor and perspectival congruency as tested with a linear mixed model with ANC score as dependent variable and interaction between conditions and functional connectivity strength between insula and the other ROIs as independent variable. *,*** indicates significance level with p-value <0.05 and <0.001 respectively. N = 26 young healthy participants from Experiment 2. Insula is displayed in red on a standard MNI template from MRIcroGL.*

r = -0.12, t(23) = -0.6, p = 0.55, right insula: r = 0.07, t(23) = 0.35, p = 0.72). These results show that the insula is a brain region sensitive to BSC manipulation at encoding, which can explain part of the ANC score of participants measured a week later.

We further investigate if there was a specific functional connection with the insula and one of the other *apriori* ROIs that drove the effect. Supplementary Table 2 and 3

summarize the linear mixed model applied for each ROIs to better understand whether their functional connectivity with the insula could explain the ANC score of participants. We found a significant interaction between the conditions and the functional connection between the right insula and the right mPFC when we compared the condition encoded under visuomotor congruency, with the condition with strong visuomotor and perspectival mismatch (SYNCH1PP compared to ASYNCH3PP: estimate = -0.24, t = -3.13, p = 0.0029). Post-hoc Pearson correlations showed a significant correlation between ANC score and the functional connectivity between the right insula and right mPFC during the encoding of scene under visuomotor and perspectival congruency (SYNCH1PP: r = 0.52, t(23) = 2.95, p = 0.007). There was no significant correlation with the ANC score under strong visuomotor and perspectival mismatch (ASYNCH3PP: r = -0.19, t(23) = -0.95, p = 0.34). These results suggest that the functional connectivity between the right insula and the right mPFC at encoding explain part of the ANC score measured a week after.

3.5 Discussion

Building on previous work showing a difference in episodic content dependent on BSC manipulation (Bergouignan et al., 2014; Bréchet et al., 2019; Gauthier et al., 2020; Iriye & Ehrsson, 2022), the present study aimed to investigate the behavioral and neural correlates behind the association with the sensorimotor experience related to the encoding of an event and ANC tested one week after. We tested the effect of SoA manipulation during the encoding of virtual scenes in healthy participants and report novel findings related to the sensorimotor context at encoding. At the behavioral level, we found that the relationship between SoA and ANC depended on the sensorimotor context at encoding. Specifically, the items in the questionnaire used to measure global vividness and re-experience captured the same effect. We related this finding at the neural level with the insula, acting as a node whose functional connectivity with BSC and memory-related areas was linked with ANC depending on the sensorimotor context.

ANC is known to decrease with age (Piolino et al., 2006) and with specific conditions like Alzheimer's disease (El Haj, 2015). A few studies have shown that ANC also depends on the body context (Bergouignan et al., 2014; Gauthier et al., 2020). Here, we showed that ANC depends on the sensorimotor context at encoding and its related subjective experience, as we reported a significant interaction between SoA and ANC depending on the level of BSC manipulation experimentally induced. Under visuomotor and perspectival congruency, ANC was positively related to SoA, meaning that a poor SoA at encoding would lead to poor ANC a week after the encoding. However, this relation was disrupted under strong visuomotor and perspectival mismatch. Although both SoA and ANC are self-reported measures subject to suggestibility bias (Donaldson & Grant-Vallone, 2002), these results are unlikely to be due to such bias, as the positive relationship between SoA and ANC was found only under visuomotor and perspectival congruency. A recent study showed that items encoded before an emotionally salient event were better retained (Dunsmoor et al., 2015; Patil et al., 2017). A similar effect was found for BSC: events encoded in VR prior to the naturalistic 1PP view were better retrieved than event encoded prior an altered BSC state (no body view), suggesting that a preserved BSC improve the consolidation of long-term EAM (Bréchet et al., 2020). Building on these findings, we speculate that the encoding of the virtual scene under visuomotor and perspectival congruency was more consolidated than the encoding of the scenes under visuomotor and perspectival mismatch. Thus, these findings suggest that the recollective experience under visuomotor and perspectival congruency is related to its subjective experience at encoding.

The positive relationship between ANC and the bodily-related subjective experience was specific to SoA as we did not find similar results with SoO. The impacts of SoO on ANC has been demonstrated in a recent study (Iriye & Ehrsson, 2022). Using visuotactile stimuli, the researcher tested the effect of the encoding of scene under strong SoO (visuotactile congruency between an observed avatar and the participant), and decreased SoO (visuotactile

mismatch) and showed a reduced ANC score under decreased SoO. In our study, we did not find any relationship between SoO and ANC. We speculate that this absence of relationship is due to the fact that our BSC manipulation mainly modulated SoA, and not SoO.

Past research has also demonstrated ANC changes when adopting a 3PP instead of a 1PP at encoding (Bergouignan et al., 2014; Iriye & Jacques, 2018; Iriye & St. Jacques, 2021). Although these findings provided empirical evidence towards the role of BSC on ANC, it was still arguable that the changes of ANC was due to a change of pure visual stimuli instead of changes of BSC states. However, we found no significant interaction in this study when comparing our two altered BSC conditions, providing new evidence that the strength of recollection is less likely to be attributed to a pure visual stimuli modulation. Finally, Bréchet and colleagues (Bréchet et al., 2019), demonstrated that there was no difference of recognition performance when encoding a scene with an object observed from a 1PP compared to no object. Together, our results are in line with the literature and brought additional evidence to show that ANC does not depends on change of visual stimuli only, but depends on changes of subjective experience related to BSC.

At the neural level, functional changes between the right parahippocampus and hippocampus as measured by peri-encoding resting-state functional connectivity were related to the change of naturalistic viewpoint adopted at encoding (Gauthier et al., 2020). We did not find a significant difference between conditions during the encoding of an event when investigating the changes of functional connectivity between our *apriori* network of interest (bilateral hippocampus, parahippocampus, mPFC, insula, angular gyrus, precuneus, SMA, and left dPMC). However, the study reporting such changes compared participants' resting state functional connectivity before and after encoding (Gauthier et al., 2020), while our analysis targeted the functional connectivity during encoding. Moreover, ANC was measured a week after encoding. Therefore, it is possible that part of the effect observed behaviorally was due to consolidation process arising after the encoding session and was hence not captured in the brain activity at encoding (Dewar et al., 2014; Martini et al., 2018).

When investigating the association between ANC and the functional connectivity of the *apriori* network at encoding, we showed that the bilateral insula acted as a node sensitive to sensorimotor integration during encoding. Similar to its association with SoA, ANC was higher when the functional connectivity of the insula with our apriori network of interest was stronger. Critically, this association was specific to the successful integration of the multisensory and sensorimotor context, as we found this relationship only under visuomotor and perspectival congruency. We chose the insula in our *apriori* network of interest because of its involvement in BSC (Ferri et al., 2012; Park & Blanke, 2019). Previous studies have highlighted the difference of activity and functional connectivity of the insula related to changes of BSC states (Karnath & Baier, 2010; Ronchi et al., 2015). Here we showed that its functional connectivity with memory-related areas plays a role at encoding in ANC processes and is impacted by BSC manipulation. Our results showed that over the fifteen *apriori* brain regions chosen in our analysis, only the insula displayed significant functional connectivity

changes with BSC manipulation that could explain ANC. As we used stringent statistical corrections and a rather extended number of *apriori* brain regions, these corrections may hide the links between other ROIs as important nodes to mediate BSC and ANC.

Interestingly, we found that the functional connection between the right insula and the right mPFC explained the ANC score of participants when the scene encoded was under visuomotor and perspectival congruency. The mPFC is known to be involved in episodic memory retrieval and more specifically, in ANC processes (Blum et al., 2006; Preston et Eichenbaum, 2013; Simons et Spiers, 2003). Its activity has also been related to self-related process such as mental imagery and self-identification (Gusnard et al., 2001; Keenan et al., 2000). Here, our results indicate that this region is also involved with BSC-related processes and that its link with the right insula explains part of the ANC score of participants. Together our results showed that under successful sensorimotor integration, the functional connectivity between BSC and memory-related brain regions can explain the strength of recollection of participants, measured a week after.

The present study measured ANC in virtual scenarios encoded with different levels of sensorimotor manipulation. Using VR enabled to better control the different parameters at encoding (Pan & Hamilton, 2018) and to create scenario that could not be performed in real life (Sanchez-Vives & Slate, 2005; Tajadura-Jiménez et al., 2018). The main downside of this approach was that the event encoded are considered less rich than events encoded in real-life (Smith, 2019). In our subfactor analysis, we did not find a significant association between SoA and items in the questionnaire related to reflective aspect of ANC (i.e "I remember what I thought at the time of the event", "I remember what I felt"). We interpreted this absence of association as a technical limitation in the experimental setup. Indeed, the scenes encoded in this study were uneventful except for the observation of objects and a right arm movement of an avatar. Therefore, it is less likely that these scene tiriggered personally relevant thoughts at the time of encoding. However, ANC is thought to be tightly linked with the spatial representation of a scene (Rubin & Umanath, 2015). This is what we found in our subfactor analysis, for which the questions related to the global vividness and re-experience were capturing the same effect as our complete questionnaire (positive relationship between SoA and ANC under visuomotor and perspectival congruency). These findings show that these questions were sufficient to measure ANC in our virtual scenario. Our results demonstrated that VR is a suitable tool to measure the effect of BSC manipulation on ANC, but the richness of the VR will affect the different questions used to measure ANC.

To conclude, this study demonstrated that the ANC process is sensitive to changes in sensorimotor integration while encoding virtual scenes. This process seems to be mediated by the interaction of the insula with memory and BSC-related areas at encoding. Together these results shed light on how the sensorimotor aspect of BSC at encoding impacts ANC.

3.6 References

Bergouignan, L., Nyberg, L., & Ehrsson, H. H. (2014). Out-of-body–induced hippocampal amnesia. *Proceedings of the National Academy of Sciences*, *111*(12), 4421-4426. https://doi.org/10.1073/pnas.1318801111

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature Reviews Neuroscience*, *13*(8), Art. 8. https://doi.org/10.1038/nrn3292

Blanke, O., & Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. *Trends in Cognitive Sciences*, *13*(1), 7-13. https://doi.org/10.1016/j.tics.2008.10.003

Blanke, O., Slater, M., & Serino, A. (2015). Behavioral, Neural, and Computational Principles of Bodily Self-Consciousness. *Neuron*, *88*(1), 145-166. https://doi.org/10.1016/j.neuron.2015.09.029

Bonnici, H. M., Cheke, L. G., Green, D. A. E., FitzGerald, T. H. M. B., & Simons, J. S. (2018). Specifying a Causal Role for Angular Gyrus in Autobiographical Memory. *Journal of Neuroscience*, *38*(49), 10438-10443. https://doi.org/10.1523/JNEUROSCI.1239-18.2018

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

Bréchet, L., Grivaz, P., Gauthier, B., & Blanke, O. (2018). Common Recruitment of Angular Gyrus in Episodic Autobiographical Memory and Bodily Self-Consciousness. *Frontiers in Behavioral Neuroscience*, *12*. https://www.frontiersin.org/articles/10.3389/fnbeh.2018.00270

Bréchet, L., Mange, R., Herbelin, B., Theillaud, Q., Gauthier, B., Serino, A., & Blanke, O. (2019). First-person view of one's body in immersive virtual reality : Influence on episodic memory. *PLOS ONE*, *14*(3), e0197763. https://doi.org/10.1371/journal.pone.0197763

Cabanis, M., Pyka, M., Mehl, S., Müller, B. W., Loos-Jankowiak, S., Winterer, G., Wölwer, W., Musso, F., Klingberg, S., Rapp, A. M., Langohr, K., Wiedemann, G., Herrlich, J., Walter, H., Wagner, M., Schnell, K., Vogeley, K., Kockler, H., Shah, N. J., … Kircher, T. (2013). The precuneus and the insula in self-attributional processes. *Cognitive, Affective, & Behavioral Neuroscience*, *13*(2), 330-345. https://doi.org/10.3758/s13415-012-0143-5

Crema, A., Bassolino, M., Guanziroli, E., Colombo, M., Blanke, O., Serino, A., Micera, S., & Molteni, F. (2022). Neuromuscular electrical stimulation restores upper limb sensory-motor functions and body representations in chronic stroke survivors. *Med*, *3*(1), 58-74.e10. https://doi.org/10.1016/j.medj.2021.12.001

Dewar, M., Alber, J., Cowan, N., & Sala, S. D. (2014). Boosting Long-Term Memory via Wakeful Rest : Intentional Rehearsal Is Not Necessary, Consolidation Is Sufficient. *PLOS ONE*, *9*(10), e109542. https://doi.org/10.1371/journal.pone.0109542

Donaldson, S. I., & Grant-Vallone, E. J. (2002). Understanding Self-Report Bias in Organizational Behavior Research. *Journal of Business and Psychology*, *17*(2), 245-260. https://doi.org/10.1023/A:1019637632584

El Haj. (2015). *Phenomenological Reliving and Visual Imagery During Autobiographical Recall in Alzheimer's Disease—IOS Press*. https://content.iospress.com/articles/journal-of-alzheimers-disease/jad151122

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

Ferri, F., Frassinetti, F., Ardizzi, M., Costantini, M., & Gallese, V. (2012). A Sensorimotor Network for the Bodily Self. *Journal of Cognitive Neuroscience*, *24*(7), 1584-1595. https://doi.org/10.1162/jocn_a_00230

Freton, M., Lemogne, C., Bergouignan, L., Delaveau, P., Lehéricy, S., & Fossati, P. (2014). The eye of the self : Precuneus volume and visual perspective during autobiographical memory retrieval. *Brain Structure and Function*, *219*(3), 959-968. https://doi.org/10.1007/s00429-013-0546-2

Freude, H., Ressing, C., Müller, M., Niehaves, B., & Knop, M. (2020). *Agency and Body Ownership in Immersive Virtual Reality Environments : A Laboratory Study*. http://hdl.handle.net/10125/63927

Gauthier, B., Albert, L., Martuzzi, R., Herbelin, B., & Blanke, O. (2021). Virtual Reality Platform for Functional Magnetic Resonance Imaging in Ecologically Valid Conditions. *Proceedings of the 27th ACM Symposium on Virtual Reality Software and Technology*. https://doi.org/10.1145/3489849.3489894

Gauthier, B., Bréchet, L., Lance, F., Mange, R., Herbelin, B., Faivre, N., Bolton, T. A. W., Ville, D. V. D., & Blanke, O. (2020). First-person body view modulates the neural substrates of episodic memory and autonoetic consciousness : A functional connectivity study. *NeuroImage*, *223*, 117370. https://doi.org/10.1016/j.neuroimage.2020.117370

Grimshaw,G.M, N., M. E. (2013). *The Flinders Handedness survey (FLANDERS) : A brief measure of skilled hand preference | Elsevier Enhanced Reader*. https://doi.org/10.1016/j.cortex.2013.02.002

Gusnard, D. A., Akbudak, E., Shulman, G. L., & Raichle, M. E. (2001). Medial prefrontal cortex and self-referential mental activity : Relation to a default mode of brain function. *Proceedings of the National Academy of Sciences*, *98*(7), 4259-4264. https://doi.org/10.1073/pnas.071043098

Heydrich, L., & Blanke, O. (2013). Distinct illusory own-body perceptions caused by damage to posterior insula and extrastriate cortex. *Brain*, *136*(3), 790-803. https://doi.org/10.1093/brain/aws364

Hoover, A. E. N., & Harris, L. R. (2016). Inducing ownership over an 'other' perspective with a visuo-tactile manipulation. *Experimental Brain Research*, *234*(12), 3633-3639. https://doi.org/10.1007/s00221-016-4760-z

Irish. (2008). *Assessment of behavioural markers of autonoetic consciousness during episodic autobiographical memory retrieval : A preliminary analysis—IOS Press*. https://content.iospress.com/articles/behavioural-neurology/ben00190

Irish. (2011). *Elsevier Enhanced Reader*. https://reader.elsevier.com/reader/sd/pii/S0028393211002661?token=890DE9E7DA8CDEC9F30F0D25238FDC9E64A0DFEB84F38ECCC7A4BCD88645A1D3B4FBBC18DA7F42C86EC9C0023590A66A&originRegion=eu-west-1&originCreation=20221004220842

Iriye, H., & Ehrsson, H. H. (2022). Perceptual illusion of body-ownership within an immersive realistic environment enhances memory accuracy and re-experiencing. *IScience*, *25*(1), 103584. https://doi.org/10.1016/j.isci.2021.103584

Iriye, H., & Jacques, P. L. S. (2018). *Construction and Elaboration of Autobiographical Memories from Multiple Visual Perspectives* (p. 317594). bioRxiv. https://doi.org/10.1101/317594

Iriye, H., & St. Jacques, P. L. (2021). Memories for third-person experiences in immersive virtual reality. *Scientific Reports*, *11*(1), Art. 1. https://doi.org/10.1038/s41598-021-84047-6

Jeunet, C., Albert, L., Argelaguet, F., & Lécuyer, A. (2018). "Do You Feel in Control?" : Towards Novel Approaches to Characterise, Manipulate and Measure the Sense of Agency in Virtual Environments. *IEEE Transactions on Visualization and Computer Graphics*, *24*(4), 1486-1495. https://doi.org/10.1109/TVCG.2018.2794598

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Johnson, M. K., Foley, M. A., Suengas, A. G., & Raye, C. L. (1988). Phenomenal characteristics of memories for perceived and imagined autobiographical events. *Journal of Experimental Psychology: General*, *117*, 371-376. https://doi.org/10.1037/0096-3445.117.4.371

Kalckert, A., & Ehrsson, H. (2012). Moving a Rubber Hand that Feels Like Your Own : A Dissociation of Ownership and Agency. *Frontiers in Human Neuroscience*, *6*. https://www.frontiersin.org/articles/10.3389/fnhum.2012.00040

Kalckert, A., & Ehrsson, H. H. (2014). The moving rubber hand illusion revisited : Comparing movements and visuotactile stimulation to induce illusory ownership. *Consciousness and Cognition*, *26*, 117-132. https://doi.org/10.1016/j.concog.2014.02.003

Karnath, H.-O., & Baier, B. (2010). Right insula for our sense of limb ownership and self-awareness of actions. *Brain Structure and Function*, *214*(5), 411-417. https://doi.org/10.1007/s00429-010-0250-4

Keenan, J. P., Wheeler, M. A., Gallup, G. G., & Pascual-Leone, A. (2000). Self-recognition and the right prefrontal cortex. *Trends in Cognitive Sciences*, *4*(9), 338-344. https://doi.org/10.1016/S1364-6613(00)01521-7

Klein, S. (2013). Making the case that episodic recollection is attributable to operations occurring at retrieval rather than to content stored in a dedicated subsystem of long-term memory. *Frontiers in Behavioral Neuroscience*, *7*. https://www.frontiersin.org/articles/10.3389/fnbeh.2013.00003

Klein, S. B., Gangi, C. E., & Lax, M. L. (2011). Memory and Self-knowledge in Young Adults with ADHD. *Self and Identity*, *10*(2), 213-230. https://doi.org/10.1080/15298861003741604

Klein, S. B., & Nichols, S. (2012). Memory and the Sense of Personal Identity. *Mind*, *121*(483), 677-702. https://doi.org/10.1093/mind/fzs080

Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video Ergo Sum : Manipulating Bodily Self-Consciousness. *Science*, *317*(5841), 1096-1099. https://doi.org/10.1126/science.1143439

Lenggenhager et al.,. (2014). *The bodily self and its disorders : Neurological, psychologic... : Current Opinion in Neurology*. https://journals.lww.com/co-neurology/fulltext/2014/12000/the_bodily_self_and_its_disorders___neurological,.6.aspx

Martini, M., Martini, C., Maran, T., & Sachse, P. (2018). Effects of post-encoding wakeful rest and study time on long-term memory performance. *Journal of Cognitive Psychology*, *30*(5-6), 558-569. https://doi.org/10.1080/20445911.2018.1506457

Pan, X., & Hamilton, A. F. de C. (2018). Why and how to use virtual reality to study human social interaction : The challenges of exploring a new research landscape. *British Journal of Psychology*, *109*(3), 395-417. https://doi.org/10.1111/bjop.12290

Park, H.-D., & Blanke, O. (2019). Coupling Inner and Outer Body for Self-Consciousness. *Trends in Cognitive Sciences*, *23*(5), 377-388. https://doi.org/10.1016/j.tics.2019.02.002

Piolino, P., Desgranges, B., Clarys, D., Guillery-Girard, B., Taconnat, L., Isingrini, M., & Eustache, F. (2006). Autobiographical memory, autonoetic consciousness, and self-perspective in aging. *Psychology and Aging*, *21*(3), 510-525. https://doi.org/10.1037/0882-7974.21.3.510

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

Ronchi, R., Bello-Ruiz, J., Lukowska, M., Herbelin, B., Cabrilo, I., Schaller, K., & Blanke, O. (2015). Right insular damage decreases heartbeat awareness and alters cardio-visual effects on bodily self-consciousness. *Neuropsychologia*, *70*, 11-20. https://doi.org/10.1016/j.neuropsychologia.2015.02.010

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

Sanchez-Vives & Slate. (2005). *From presence to consciousness through virtual reality | Nature Reviews Neuroscience*.

https://www.nature.com/articles/nrn1651

Smith, S. A. (2019). Virtual reality in episodic memory research : A review. *Psychonomic Bulletin & Review*, *26*(4), 1213-1237.

https://doi.org/10.3758/s13423-019-01605-w

Stickgold, R. (2005). Sleep-dependent memory consolidation. *Nature*, *437*(7063), Art. 7063. https://doi.org/10.1038/nature04286

Tajadura-Jiménez, A., Banakou, D., Bianchi-Berthouze, N., & Slater, M. (2018). Author Correction : Embodiment in a Child-Like Talking

Virtual Body Influences Object Size Perception, Self-Identification, and Subsequent Real Speaking. *Scientific Reports*, *8*(1),

4854. https://doi.org/10.1038/s41598-018-23231-7

Trimble, M. R., & Cavanna, A. E. (2008). Chapter 3.7 The role of the precuneus in episodic memory. In E. Dere, A. Easton, L. Nadel, & J. P.

Huston (Éds.), *Handbook of Behavioral Neuroscience* (Vol. 18, p. 363-377). Elsevier. https://doi.org/10.1016/S1569-

7339(08)00220-8

Tulving, E. (1985). Memory and consciousness. *Canadian Psychology / Psychologie canadienne*, *26*, 1-12. https://doi.org/10.1037/h0080017

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., Mazoyer, B., & Joliot, M. (2002). Automated

Anatomical Labeling of Activations in SPM Using a Macroscopic Anatomical Parcellation of the MNI MRI Single-Subject Brain.

NeuroImage, *15*(1), 273-289. https://doi.org/10.1006/nimg.2001.0978

Wheeler, M. A., Stuss, D. T., & Tulving, E. (1997). Toward a theory of episodic memory : The frontal lobes and autonoetic consciousness.

Psychological Bulletin, *121*, 331-354. https://doi.org/10.1037/0033-2909.121.3.331

Xie, C., Bai, F., Yu, H., Shi, Y., Yuan, Y., Chen, G., Li, W., Chen, G., Zhang, Z., & Li, S.-J. (2012). Abnormal insula functional network is

associated with episodic memory decline in amnestic mild cognitive impairment. *NeuroImage*, *63*(1), 320-327.

https://doi.org/10.1016/j.neuroimage.2012.06.062

Joshi, K. D., & Nalwade, P. S. (2013). Modified k-means for better initial cluster centres. *International Journal of Computer Science and Mobile Computing*, *2*(7), 219-223.

 RStudio Team (2022). RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Douglas Bates, Martin Maechler, Ben Bolker, Steve Walker (2015), Fitting Linear Mixed-Effects Models Using lme4. Journal ofStatistical Software, 67(1), 1-48. doi:10.18637/jss.v067.i01

Kuznetsova A, Brockhoff PB, Christensen RHB (2017). "lmerTestPackage: Tests in Linear Mixed Effects Models." _Journal of Statistical Software_, *82*(13), 1-26. doi:10.18637/jss.v082.i13 https://doi.org/10.18637/jss.v082.i13

Raiche G, Magis D (2020). nFactors: Parallel Analysis and Other Non Graphical Solutions to the Cattell Scree Test_. R package version 2.4.1, https://CRAN.R-project.org/package=nFactors

Kassambara A, Mundt F (2020). factoextra: Extract and Visualize the Results of Multivariate Data Analyses_. R package version 1.0.7, https://CRAN.R-project.org/package=factoextra

Kassambara A (2020). ggpubr: 'ggplot2' Based Publication Ready Plots_. R package version 0.4.0, <https://CRAN.R-project.org/package=ggpubr>

3.7 Supplementary Information

Familiarization

Prior to the encoding session, participants were immersed in the four scenes (three encoding scenes and the BSC scene) but emptied from all the objects being part of the later recognition task. They were instructed to move their hands and observe the scene for 15 seconds after which they were asked one binary question "2 plus 2 equal 4", followed by a second question "How confident are you about your answer" in order to train to the two types of questions that would be asked during the experiment. Finally, they were asked to move their right arm for 30 seconds to train them for the rest of the experiment. During this time, when necessary, we interacted with the participant to tell them if the movement was too fast or not having an amplitude big enough. Each participant started the familiarization in the BSC scene in the SYNCH1PP condition.

Identification of brain regions sensitive to BSC manipulation during encoding

To identify the brain regions sensitive to our BSC manipulation during encoding, we compared the brain activity under visuomotor and perspectival congruency at encoding (SYNCH1PP) with the conditions in which induced and visuomotor and perspectival mismatch (ASYNCH1PP and ASYNCH3PP). We first built first-level contrast map for each participant after which we performed a group analysis using the contrast (2*SYNCH1PP> ASYNCH1PP+ASYNCH3PP). We used a cluster-defining threshold of $p < 0.001$ uncorrected combined with a False Discovery Rate (FDR) cluster-level correction with a threshold of $p < 0.05$ to account for multiple comparisons. We then parcellated the cluster onto three different ROIs using the automated anatomical labeling atlas (aal; Tzourio-Mazoyer et al., 2002).

Effect of conditions on sense of ownership and threat

Participants had a significantly higher SoO in the SYNCH1PP condition compared to the ASYNCH3PP condition (estimate = -0.12, t = -4.93, $p < 0.001$). We found that the ratings were significantly lower in Experiment 2 compared to Experiment 3 (estimate = -0.13, t = -2, p =0.04). As Experiment 2 was in the real MR scanner, it might have decreased the level of SoO of participants due to the MR noise. Similarly to the SoO ratings, participants were significantly more afraid towards a virtual threat when observed in SYNCH1PP compared to ASYNCH3PP (estimate = -0.2, t = -5.8, p = <0.001). There was no significant difference when comparing SYNCH1PP and ASYNCH1PP (SoO: estimate = -0.003, t = -0.15, p = 0.83; Threat estimate = -0.03, t = 0.97, p = 0.33)

	FC X Conditions SYNCH1PP vs ASYNCH1PP			FC X Conditions SYNCH1PP vs ASYNCH3PP			FC X Conditions ASYNCH1PP vs ASYNCH3PP		
	estimate	t	p	estimate	t	p-value	estimate	t	p
Hippocampus left	-0.01	-1.19	0.23	0.01	1.21	0.22	0.03	2.3	0.02
Hippocampus right	0.007	0.54	0.58	0.02	1.47	0.14	0.013	0.9	0.37
PHC left	0.001	0.1	0.91	0.008	0.55	0.58	0.006	0.43	0.67
PHC right	-0.025	-1.7	0.08	-0.004	-0.29	0.77	0.02	1.4	0.17
mPFC left	0.003	0.29	0.77	0.002	-0.47	0.85	-0.001	-0.16	0.87
mPFC right	0.006	-0.6	0.54	0.008	-0.7	0.45	-0.008	0.07	0.93
Insula left	-0.007	-0.6	0.03	**-0.06**	**-4.36**	**<0.0001**	**-0.06**	**-3.6**	**0.0003**
Insula right	-0.018	-1.4	0.15	**-0.04**	**-3.33**	**0.0008**	-0.02	-1.8	0.07
Angular gyrus left	-0.014	-1.4	0.16	-0.014	-0.13	0.89	0.01	1.18	0.23
Angular gyrus right	-0.005	-0.42	0.67	0.007	0.64	0.52	0.01	0.98	0.32
Precuneus left	0.002	0.2	0.8	0.007	0.7	0.4	0.005	0.48	0.63
Precuneus right	0.005	0.46	0.65	0.01	1	0.27	0.006	0.57	0.56
dPMC left	0.04	2.5	0.01	0.01	0.8	0.42	-0.02	-1.66	0.09
SMA left	-0.01	-0.8	0.41	-0.02	-1.6	0.86	-0.01	-1.05	0.29
SMA right	-0.007	-0.58	0.55	-0.03	-2.35	0.01	-0.02	1.7	0.09

Supplementary Table 1: Linear mixed model to explain autonoetic consciousness score by conditions, functional connectivity value and regions of interest. Summary of the results of the interactions of the model interest (ANC score ~Conditions x Functional connectivity). The bold line indicates significant results after correction for multiple comparisons ($p_{corrected}$ = 0.05/15 = 0.003). FC = functional connectivity, t = t-statistic, p = p-value (significant threshold),PHC = parahippocampus, mPFC = medial prefrontal cortex, dPMC = dorsal premotor cortex, SMA = supplementary motor area.

	FC X Conditions SYNCH1PP vs ASYNCH1PP			FC X Conditions SYNCH1PP vs ASYNCH3PP			FC X Conditions ASYNCH1PP vs ASYNCH3PP		
	estimate	t	p	estimate	t	p-value	estimate	t	p
Hippocampus left	-0.11	-1.4	0.17	-0.06	-0.6	0.55	0.05	0.48	0.63
Hippocampus right	-0.05	-0.6	0.55	-0.18	-1.84	0.07	-0.12	-1.17	0.25
PHC left	-0.03	-0.45	0.65	-0.14	-1.8	0.08	-0.1	-1.37	0.17
PHC right	0.01	0.12	0.9	-0.06	-0.7	0.48	-0.07	0.72	0.47
mPFC left	-0.04	-0.53	0.6	-0.19	-2.6	0.01	-0.15	-2.11	0.04
mPFC right	-0.05	-0.59	0.55	-0.18	-2.4	0.02	-0.14	-1.88	0.06
Insula right	0.09	1.14	0.3	-0.006	-0.08	0.99	-0.09	-1.27	0.21
Angular gyrus left	-0.07	-1.07	0.29	-0.13	-1.8	0.07	-0.05	-0.7	0.49
Angular gyrus right	-0.09	-1.15	0.25	-0.11	-1.77	0.08	-0.016	0.19	0.85
Precuneus left	-0.07	-0.83	0.4	-0.16	-2.14	0.37	-0.09	-1.02	0.3
Precuneus right	-0.01	-0.16	0.86	-0.1	-1.5	0.14	-0.09	-0.99	0.32
dPMC left	-0.01	-0.17	0.87	-0.09	-1.01	0.32	-0.07	-0.68	0.49
SMA left	0.01	0.17	0.86	-0.09	-1.01	0.31	-0.1	-1.14	0.26
SMA right	0.11	1.071	0.28	-0.17	-1.9	0.06	-0.28	-2.42	0.01

Supplementary Table 2: Linear mixed model to explain autonoetic consciousness score by conditions, functional connectivity value between left insula and the other regions of interest. Summary of the results of the interactions of the model interest (ANC score ~Conditions x Functional connectivity) where the functional connectivity corresponds to the connectivity between the left insula and each region of interest. The bold line indicates significant results after correction for multiple comparisons ($p_{corrected}$ = 0.05/14 = 0.0035). FC = functional connectivity, t = t-statistic, p = p-value (significant

| | FC X Conditions | | | FC X Conditions | | | FC X Conditions | | |
| | SYNCH1PP vs ASYNCH1PP | | | SYNCH1PP vs ASYNCH3PP | | | ASYNCH1PP vs ASYNCH3PP | | |
	estimate	t	p	estimate	t	p-value	estimate	t	p
Hippocampus left	-0.1	-1.1	0.27	0.02	0.17	0.87	0.12	1.02	0.31
Hippocampus right	-0.07	-0.76	0.45	-0.14	-1.27	0.21	-0.07	0.54	0.59
PHC left	-0.02	-0.2	0.8	-0.12	-1.34	0.19	0.05	0.59	0.56
PHC right	-0.04	-0.43	0.66	0.014	0.18	0.86	-0.09	0.98	0.33
mPFC left	-0.05	-0.73	0.47	-0.15	-1.9	0.06	-0.1	-1.28	0.21
mPFC right	-0.08	-1.18	-0.24	**-0.24**	**-3.13**	**0.0029**	-0.14	-1.89	0.06
Insula left	0.09	1.14	0.3	-0.006	-0.08	0.99	-0.09	-1.27	0.21
Angular gyrus left	-0.09	-1.44	0.15	-0.1	-1.58	0.12	-0.008	-0.12	0.9
Angular gyrus right	-0.08	-1.17	0.25	-0.06	-1.14	0.26	0.018	0.25	0.8
Precuneus left	-0.1	-1.27	-0.2	-0.13	-2.03	0.047	-0.03	-0.4	0.68
Precuneus right	-0.05	-0.62	0.53	-0.08	-1.2	0.23	-0.03	-0.46	0.65
dPMC left	-0.08	-0.71	0.48	-0.04	-0.45	0.65	0.03	0.27	0.79
SMA left	0.05	0.56	0.58	-0.08	-0.92	0.36	-0.14	-1.3	0.2
SMA right	-0.03	-0.34	0.74	-0.22	-2.2	0.03	-0.19	-1.55	0.13

Supplementary Table 3: **Linear mixed model to explain autonoetic consciousness score by conditions, functional connectivity value between right insula and the other regions of interest.** *Summary of the results of the interactions of the model interest (ANC score ~Conditions x Functional connectivity), where the functional connectivity corresponds to the connectivity between the right insula and each region of interest. The bold line indicates significant results after correction for multiple comparisons ($p_{corrected}$ = 0.05/14 = 0.0035). FC = functional connectivity, t = t-statistic, p = p-value (significant threshold), PHC = parahippocampus, mPFC = medial prefrontal cortex, dPMC = dorsal premotor cortex, SMA = supplementary motor area.*
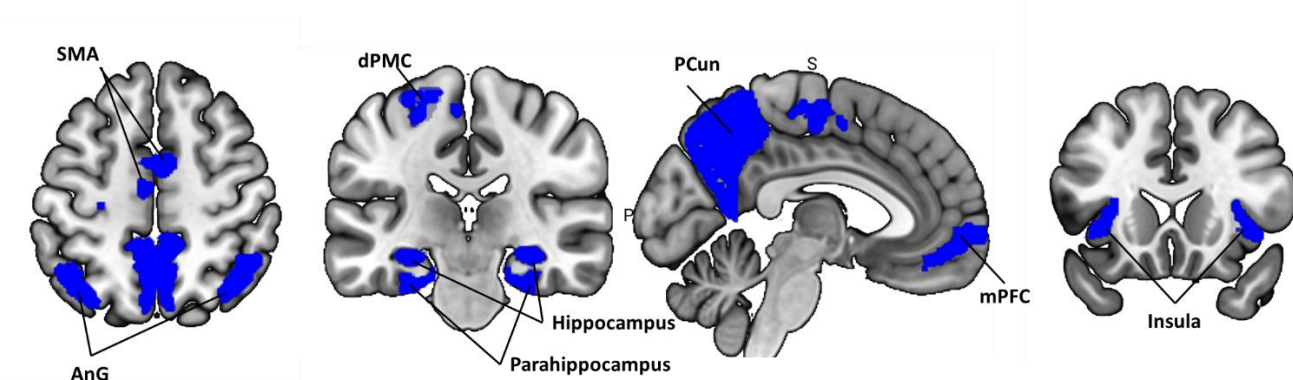

Supplementary Figure 1: *A priori network used for the ROI-to-ROI analysis to investigate the difference of functional connectivity between BSC conditions. Supplementary areas (SMA), angular gyrus (AnG), dorsal premotor cortex (dPMC), precuneus (PCun), medial prefrontal cortex (mPFC), insula, parahippocampus and hippocampus.*

4. Study 3: Altered association between bodily self-consciousness and episodic autobiographical memory in a rare case of amnesic patient

Authors

Nathalie H. Meyer[1]*, Mariana Babo-Rebelo[1]*, Jevita Potheegadoo[1], Bruno Herbelin[1], Sara Stampacchia[1], Fabienne Esposito[2], Marilia Morais Lacerda[2], Arthur Trivier[1], Florian Lance[1], Elena Beanato[3], Vincent Alvarez[4], Michela Bassolino[5], Olaf Blanke[1,5]

Affiliations

[1] Laboratory of Cognitive Neuroscience, Neuro-X Institute & Brain Mind Institute and Center for Neuroprosthetics, Faculty of Life Sciences, Ecole Polytechnique Fédérale de Lausanne, Geneva, Switzerland

[2] Clinique Romande de Réadaptation, SUVA,Avenue Grand Champsec 90, 1950 Sion, Switzerland

[3] UPHUMMEL lab, Neuro-X Institute & Brain Mind Institute and Center for Neuroprosthetics, Faculty of Life Sciences, Ecole Polytechnique Fédérale de Lausanne, Geneva, Switzerland

[4] Hopital du Valais, Avenue Grand Champsec 80, 1950 Sion, Switzerland

[5] School of Health Sciences, Haute École spécialisée de Suisse occidentale (HES-SO) Valais-Wallis, Sion, Switzerland.

[6] Department of Clinical Neurosciences, University Hospital Geneva, Rue Micheli-du-Crest 24, 1205, Geneva Switzerland

*Equal contributions

4.1 Abstract

Episodic autobiographical memory (EAM) is often associated with self-consciousness as it involves the conscious recollection of personal past experiences. However, little empirical evidence shows how those two processes are linked together. As EAM relies on sensory information and subjective experience at encoding, we proposed that self-consciousness and EAM are mediated by bodily self-consciousness (BSC), a lower-level form of self-consciousness arising from the multisensory and sensorimotor integration of bodily signals. Using immersive virtual reality and state-of-the-art technology to induce bodily illusion, we tested a single case patient with severe retrograde amnesia and moderate anterograde amnesia under different BSC states. We report that the patient had more difficulty recollecting information encoded under stable BSC state than altered BSC state. At the neural level, resting state functional connectivity underlined decreased connectivity between bilateral hippocampus and bilateral parahippocampus and increased connectivity between bilateral precuneus and medial prefrontal cortex, when compared to age- and gender-match control. These results demonstrate a modulation in the recollection of EAM dependent on BSC states.

4.2 Introduction

Autobiographical memory, the memory of personal past events subscribed in one's personal history, is a building block of self-consciousness (Markowitsch & Staniloiu, 2011; Tulving, 1985; Wang & Conway, 2006). Autobiographical memory is composed of memories of contextually rich events personally experienced called episodic autobiographical memory (EAM), and memories of general self-knowledge, independent of their encoding context, called semantic autobiographical memory (Tulving, 1985). This dichotomy has been supported by several cases of retrograde amnesia with specific deficits in EAM and preserved semantic autobiographical memory (De Renzi et al., 1997; Illman et al., 2011; Kapur et al., 1992; Levine et al., 1998, 2009; Mayes et al., 2003; Piolino et al., 2005). Studies investigating EAM often focused on the retrieval of the spatiotemporal context using the famous "What"-"Where"-"When" questions, to measure the memory accuracy of an event ("What"), in a spatial ("Where") and temporal ("When") context (Holland and Smulders 2011). But EAM retrieval also involves the re-experience of sensory details and mental states associated with an event, a process called autonoetic consciousness (Tulving, 1985; M. A. Wheeler et al., 1997).

According to the Multiple Trace Theory (MTT), the recollection of contextually rich memory remains dependent of the hippocampus, while the general information of a memory, independent of its context are gradually stored in the neocortex and becomes independent from the hippocampus (Brodt et al., 2018; Lavenex & Amaral, 2000; Moscovitch et al., 2016; Robin & Moscovitch, 2017). Several clinical cases highlight the role of the hippocampus and prefrontal cortex in this linkage (Gomez et al., 2012; Illman et al., 2011; S. B. Klein & Nichols, 2012).

Notably, integration of the multisensory and sensorimotor information gathered during the experience of an event is the substrate for the sense of bodily self-conscioussness (BSC). BSC give rise to the experience of a unitary self within the body boundaries (Blanke, 2012; Blanke et al., 2015; Blanke & Metzinger, 2009; Tsakiris et al., 2007). This opens the possibility that EAM also relates to a more low-level and bodily dimension of the self, i.e. bodily self-consciousness (BSC).

BSC is considered to include four building blocks - a sense of ownership (the feeling that the body belongs to oneself), a sense of agency (the feeling that one is in control of his/her own body), a sense of self-location (the feeling that the "self" is located within the body boundaries) and first-person perspective (1PP, the feeling of seeing the world from the location of one's body, in a naturalistic perspective). Although this unitary sense of BSC seems trivial, these four building blocks of BSC are reported to be altered in some clinical conditions (Blanke & Castillo, 2007; Blanke & Mohr, 2005; Jeannerod, 2009; Maeda et al., 2013). The use of virtual reality (VR) enabled to boost research on BSC by inducing temporary bodily illusions in healthy participants using sensory mismatch (Kilteni et al., 2012, Lenggenhager et al., 2014). One famous example is the full-body illusion (FBI), in which a participant observes an avatar

back in VR. When the avatar back is stroke synchronously with the participant's back, this triggers a shift of the participant's self-location towards the avatar back. In other words, this experiment uses visuotactile congruency to trigger the embodiment of the avatar by the participant. The role of BSC in EAM is still poorly understood. By manipulating multisensory and sensorimotor integration, often with VR, some studies have shown initial evidence for an implication of BSC in encoding episodic memories. For example, encoding an event from a 1PP gives rise to stronger episodic memories than encoding an event at the third-person perspective (3PP; Bergouignan et al., 2014). Consistently with this finding, our group showed a decrease in EAM accuracy when an event was encoded without a body view compared to an event encoded from a 1PP, which was related to reduced peri-encoding resting state functional connectivity between the right hippocampus and parahippocampus (Bréchet et al., 2019; Gauthier et al., 2020). Although these studies provide meaningful insight into the impact of BSC on EAM little is known about the neural substrate involved in this association.

In this study, we report the rare case of a patient with bilateral lesions in the hippocampus and adjacent regions following brain infection, which lead to severe retrograde and mild anterograde amnesia specific for EAM. In two experiments using immersive VR and real life like scenarios, we investigated how a manipulation of BSC affects the recollection of information for scenes newly encoded. In Experiment 1, we manipulated the visuomotor congruency between an observed virtual avatar moving synchronously or asynchronously with one's movements, thereby triggering a sense of ownership and agency of the virtual body in the synchronous condition (Imaizumi & Asai, 2015; Padilla-Castañeda et al., 2014). In Experiment 2, we induced an FBI to manipulate BSC and its related sense of self-location in the patient. Based on the patient's lesions, we hypothesized that BSC would be preserved in the patient. We measured EAM and autonoetic consciousness in each experiment for each condition and investigated how it was impacted by the BSC manipulation in this patient.

4.3 Methods

Clinical description

In this study, we report the rare case of a 62 years old female patient (french speaker, right-handed) suffering from a moderate to severe autobiographical episodic memory deficit following a fungal brain infection (aspergillosis meningoencephalitis) with focal brain damage in bilateral hippocampi and adjacent regions. On the date of the diagnosis, the patient had three foci of infection: right frontal, right temporal, and left parietal. The patient had lesions on the right hippocampus as observed on a clinical T2. Two days later, the lesions were observed bilaterally on the hippocampus and adjacent regions such as amygdala and parahippocampus (**Figure 1**). Following her diagnosis, the patient suffered from severe to moderate epileptic crisis, which gradually decreased in amplitude and frequency but did not disappear.

Before meningoencephalitis, the patient had no known memory or other neuropsychological issues. Following her diagnosis, the patient could not recall essential elements of her life that happened in her past (travels, wedding). She worked with a team of neuropsychologists to reconstruct a "timeline" of her history, after which she re-learned the critical events of her life. However, when asked about it, the patient could not re-experience any of these events, showing an apparent deficit of EAM. We tested the patient eight (Experiment 1) and eleven (Experiment 2) months after her diagnosis. The patient provided written informed consent following the local ethical committee (Cantonal Ethical Committee of Geneva: 2015-00092, and Vaud and Valais: 2016-02541) and the declaration of Helsinki (2013).

Neuropsychological assessment

Three months after her diagnosis, the patient was tested by trained neuropsychologists to build a neuropsychological profile and understand the extent of her memory deficit. The patient performed a battery of tests to measure working memory (Wechsler, 2008), confabulation (Dalla Barba et al., 2018), semantic memory (Moore et al., 2022), episodic memory (Van der Linden et al., 2006; Wilson et al., 2008, 2010), autobiographical memory (TEMPau test; Piolino et al., 2008) and memory for public events and celebrities (Puel et al., 2016)[1]. The patient showed normal short-term working memory, absence of confabulation, and normal semantic memory. However, the patient performed below the norm when recalling a list of words one week after encoding, and when recalling dates and places. Her EAM was severely impaired with low score on the TEMPau test and her memory for public events and celebrities was also affected.

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[1]*We are still waiting on the raw neuropsychological data from the hospital*
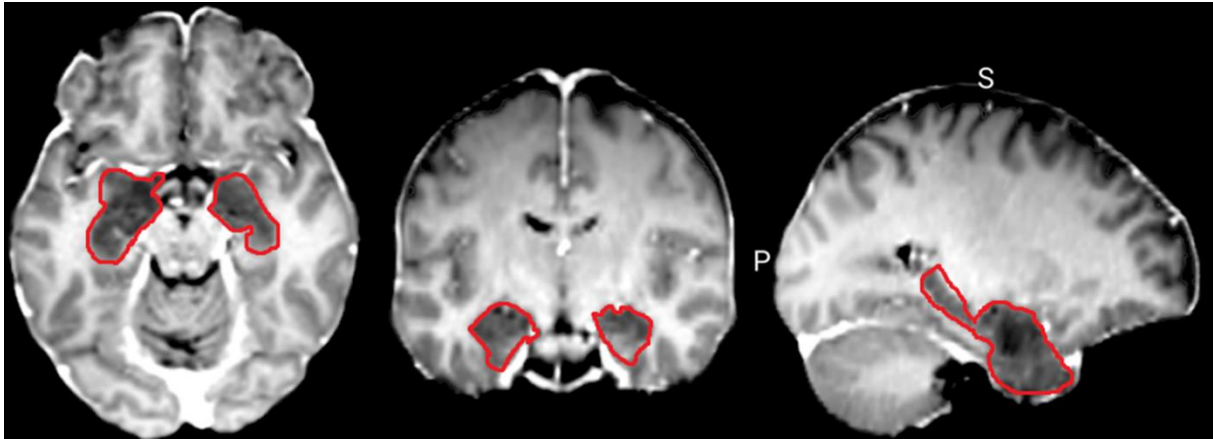
Figure 1. Patient's lesions. *bilateral lesions (circled in red) in the amygdalo-hippocampal complex on the day of the diagnosis.*

To obtain a neuropsychological profile closer to the date of our experimental procedure, a trained neuropsychologist from our lab tested the patient one month after Experiment 1 (and two months before Experiment 2). The patient was tested for her episodic memory with the Rey Auditory Verbal Learning Test (RAVLT) of List B (Rey, 1941). We tested her executive function using the Trail Making test part A and B (Reitan & Wolfson, 1985), and the Frontal Assessment Battery (FAB, Dubois et al., 2000). Finally, her autobiographical memory score was assessed using the autobiographical fluency test (Dritschel et al., 1992). A detailed description of the tests is described in the supplementary section.

Investigation of BSC impact on EAM with bilateral lesions in the hippocampal complex

We tested the patient five months after her diagnosis in a previous study (Meyer&Gauthier, in prep), in which we found a dissociation between BSC state and episodic memory retrieval: the patient could recollect better virtual scenes encoded with a disruption of multisensory and sensorimotor integration (altered BSC states) compared to virtual scene encoded under preserved BSC state. Building on these results, we tested the patient eight months after her diagnosis (Experiment 1) and eleven months after her diagnosis (Experiment 2) to deepen the investigation of the dissociation between BSC and EAM. In Experiment 1, we immersed the patient in eight virtual scenes containing a virtual avatar. We used visuomotor and perspectival mismatch to manipulate BSC state during encoding. Half of the virtual scene were encoded under ecological BSC state and the other half were encoded under decreased BSC state. We measured the patient's EAM using autonoetic consciousness questionnaire asked one week after the encoding. In Experiment 2, we tried to reproduce the results obtained in Experiment 1 by using a different sensory mismatch to manipulate BSC. We applied a visuotactile mismatch during the encoding of eight different scenarios. One week after the encoding, we measured the patient's episodic memory using autonoetic consciousness questionnaire and questions about the scenario to quantify her memory accuracy.

Experiment 1

Eight months after her diagnosis, we immersed the patient into eight virtual scenes using a head-mounted display (HMD; Oculus Rifts S, refreshing rate 80Hz, resolution 1280 x 1440 per eye, 660 ppi), while she was sitting on a chair and her movements were tracked by an infrared camera (leapmotion) mounted on the HMD. We instructed the patient to move her right arm between two black virtual spheres when they appeared in the scene and to mind wander out loud, including describing the scene and reporting any thoughts or associations that would come to mind (**Figure 2**). Half of the scenes were seen from a first-person perspective (1PP), where the position and movements of the virtual arm matched the position and movements of the patient's arm (embodied condition). In the remaining scenes, a virtual avatar was located ahead of the virtual point of view, and its arm movements were delayed compared to the patient's movements, resulting in a third-person perspective view with asynchronous body movements (disembodied condition). Each scene was encoded for 2 min, and the patient performed the movement for 30 seconds alternating with 15 seconds of rest. Moreover, each scene was encoded with a background sound that was used as a cue during the retrieval session in case the patient had difficulties remembering the scene.
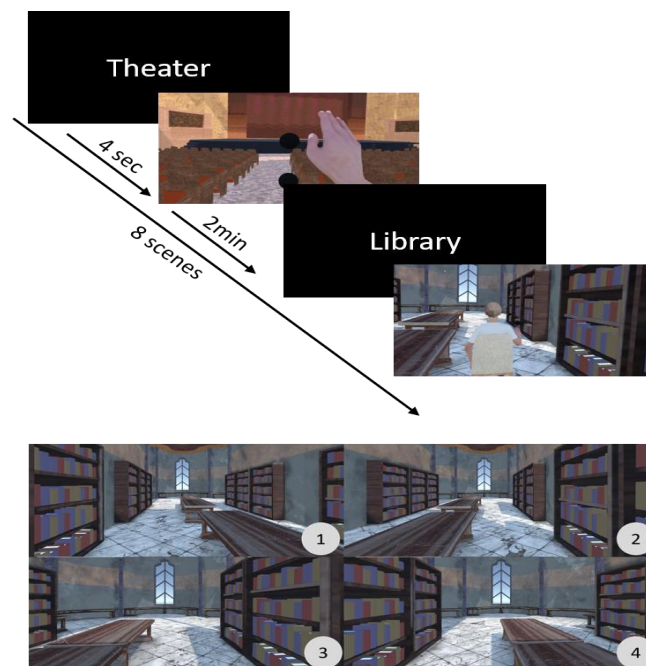

Figure 2. Experiment 1: experimental design. Patient encoded eight different virtual scenes and either viewed an avatar from the first-person perspective with synchronization between the patient and avatar's movement (embodied condition) or from the third-person perspective with a delay between patient and avatar's movement (disembodied condition).

Measure of the bodily illusion strength

To test the patient's sensitivity to the BSC manipulation, we immersed the patient in one outdoor scene in which she observed an avatar in the two encoding condition: (1) the avatar was observed in 1PP and the avatar's right arm was moving synchronously with the patient movement (embodied condition), thus being as close as possible to a naturalistic successful multisensory and sensorimotor integration. (2) the avatar was observed in 3PP and the avatar right arm movement was delayed compared to the patient's movement. This condition corresponds to a strong BSC manipulation (disembodied condition). The patient observed the avatar for 30 seconds twice in each condition. After each time, we asked her to answer four questions (continuous scale) to rate her sense of agency ("I felt that I was controlling the virtual body"), her sense of ownership ("I felt that the virtual body was mine"), and control for experimental bias ("I felt that I had more than three bodies" and "I felt that the trees were my body").

Retrieval

One week after the encoding session, we tested the patient's episodic memory for the eight virtual events in two folds. First, the patient was asked to recall each scene freely. We assessed autonoetic consciousness during recall of the scene using an in-house questionnaire (**Supplementary Table 1**), including questions from the memory characteristic questionnaire (Johnson et al., 1988) and episodic autobiographical memory interview part B (Irish et al., 2011). When the patient could not retrieve the memory using free recall, we presented the visual picture of the scene taken from four different perspectives (the avatar was removed in the picture to keep each scene neutral regarding the experimental manipulation of BSC). When this was not sufficient, we replayed the sound associated with the scene. Second, we tested the ability of the patient to remember the scene by presenting four different perspective of the scene encoded and asking her to select the perspective she experienced during encoding among them.This test was considered as an implicit measure of memory, as the patient did not have to describe the scene but just select what she thought correspond to her experience at encoding. The patient was prompted to answer even when she was not able to retrieve any detail from the scene.

Experiment 2

We tested the patient three months after Experiment 1, in an attempt to replicate the results from Experiment 1 and further investigate how different sub-components of episodic memory were link with BSC. We tested episodic memory with another type of sensory mismatch, to ensure that the effect found in Experiment 1 was not due to the specific type of stimuli but to a disruption of multisensory and sensorimotor integration. We used the FBI (Lenggenhager et al., 2007) to manipulate the sense of self-location and the sense of ownership towards the projected view of the patient's back. The stroking applied to the back of the patient could be either synchronous or asynchronous with the stroking that the patient saw on the projection of her own back (visuotactile synchrony or asynchrony). The synchronous condition usually

leads to a shift in self-location towards the projected back, being more embodied than the asynchronous condition. Critically in this setup, the visual stimuli remained almost identical between conditions, which only differed in the delay between visual and tactile stimulations.

The patient sat in a chair, wearing an HMD (Oculus Rift DK1, resolution of 640x800, horizontal FOV 90°). A camera (Logitech C510, resolution 1280x720, 30 fps) placed 2 meters behind the patient's back filmed the scene and projected it on the HMD **(Figure 3A)**. The FBI was applied for one minute. For the asynchronous condition, a delay of 500ms was added between the filmed scene and the projected scene in the HMD. During the induction, the experimenter stroked the patient's back with a wooden stick similarly as in (Lenggenhager et al., 2007). Following FBI induction, a two-minute scene was played by an actor, in front of the patient. In total, we performed 8 FBI inductions – scene sequences, in 8 different locations in our campus (new environment for the patient), during a whole day. The scenes differed in terms of the gender of the actor, successful or unsuccessful scene outcome (ex: successfully making a photocopy vs unsuccessfully trying to make a coffee), right/left visual field, straight/lateral perspective relative to the environment geometry, morning/afternoon, ground floor / upper floors and synchronous/asynchronous. Conditions were counterbalanced between scenes. (**Supplementary Figure 1**).

Figure 3. Experimental setup and example of questions on perspective recollection. A.Experimental setup. *After 1 min induction of the full-body illusion (FBI ; top panel), the patient observed an actor performing a scene either on the right or on the left of her visual field. The patient encoded 8 scenes, half of them in the embodied condition and half of them in the disembodied condition.* ***B.Perspectival questions.*** *Example of the four views presented to the patient during the retrieval session for the perspective question. The patient had to choose the view in which she encoded the scene.*

Measure of the bodily illusion strength

After encoding the eight scenes, we tested the patient's sensitivity to the induction of the bodily illusion. We induced the FBI eight times while the patient was standing and observing her back stroked from the HMD, in a neutral black room. In half of the trials, the visuotactile stimulation was congruent, which aimed to induce a shift of self-location toward the observed back. In the other trials, the visuotactile stimulation was asynchronous and was not supposed to generate the illusory self-location shift (disembodied condition). After each trial, the patient saw a black screen and the experimenter moved the patient backward with small steps. The patient was then asked to walk back to where she thought she was at the time of the FBI induction. The distance error between her perceived location and the correct one was measured.

Retrieval

We tested the patient's episodic memory one week after the encoding. For each scene, we quantified her memory in three steps. First, the patient was cued with the name of the scene (for example, "coffee machine") and was asked to recall as many details as possible from each scene freely. In a second step, we asked her eight questions to measure her autonoetic consciousness. These were related to the strength of vividness, visual details, and global and emotional reliving (questions 17-24 of **Supplementary Table 1**). These eight questions were extracted from the questionnaire asked in Experiment 1, and found to be sufficient to capture the autonoetic consciousness of young healthy participants in a previous study (Meyer et al., in prep, Chapter 3, Study 2 in the present thesis). In a third step, to have better understanding of how BSC impact the patient's memory accuracy, which was not tested in Experiment 1, we asked forced-choice questions about the spatiotemporal context of each scene, the classical "What"-"Where"-"When" content of episodic memory (Holland & Smulders, 2011). We tested the "What" (Q1: was the actor a male or a female, Q2: Did the actor succeed his/her task?), the "Where" (Q3: did the event happened on the right or left part of your field of view?, Q4: did the event happened on the ground floor or on another floor?) and the "When" (Q5: Did the event happen in the morning or in the afternoon?) dimensions of the episodes. For each question, we asked the patient to rate her confidence using a 7 point likert-scale (0: not sure of the answer, 6, totally sure of the answer) We then provided the patient with four pictures of the scene taken from four different perspectives (similar to Experiment 1) to obtain an implicit measure of her memory. We asked her to choose the one that corresponded to the perspective in which she originally encoded the scene **(Figure 3B)**.

Data analysis

In Experiment 1 and 2, we first reversed the scale of items 8, 9 and 11 from the autonoetic consciousness questionnaire (Supplementary table 1), in order to have consistency within the questionnaire items, where higher ratings correspond to a stronger recollection. We then computed the autonoetic consciousness score of the patient by summing the ratings associated with each scene to obtain one score per scene.

In Experiment 2, we quantified the memory accuracy by normalizing the number of correct answers over the total number of questions asked about the spatiotemporal context of each scene.

Statistical analysis

This study reports two experiments performed by a single patient with a rare condition which makes it worth it testing despite the difficulty in statistically supporting the results. Hence, all the behavioral results described here can be considered as qualitative observations. We considered that replicating the results in two experiments would give strength to the results despite the lack of statistical analyses.

For a better understanding of the data, we normalized the confidence and autonoetic consciousness ratings.

Resting-state fMRI

MRI acquisition

One month after Experiment 1, we recorded the resting state functional activity of the patient. MR images of the patient were acquired using a 3T MRI scanner (MAGNETOM PRISMA; Siemens) using a 64-channel head coil. First a 5 min anatomical imaging was acquired using a T1-weighted MPRAGE sequence (TR = 2300 ms, TE = 2.25 ms, TI = 900 ms, Slice thickness = 1 mm, In-plane resolution = 1 mm × 1 mm, Number of slices = 208, FoV = 256 mm, Flip angle = 8). Resting-state fMRI was acquired using a gradient echo echo planar sequence (TR = 1500ms, TE = 3 ms, Slice thickness = 2mm, number of slices = 69, in-plane resolution = 2 mm × 2 mm, Multiband factor = 3, slice acquisition order = interleaved). We compared the functional connectivity of the patient during rest with the resting state of 23 healthy females (mean age = 62.4 ± 4) obtained from the Alzheimer's Disease Neuroimaging Initiative (ADNI) database (adni.loni.usc.edu). We selected female participants from the ADNI study which were labeled as controls, aged between 55 to 67 (to be as close as possible of the patient's age) and for which T1 and resting state (with eyes open) were acquired with a 3T MRI scanner manufactured from Siemens and a TR of 3 seconds. Data were preprocessed using the standard default processing of the conn toolbox version 20b (www.nitrc.org/projects/conn), including slice timing correction, realignment, segmentation, normalization to MNI plane, and smoothing (Nieto-Castanon, 2020).

ROI-to-ROI analysis

To investigate the resting functional connectivity of the patient, we performed an ROI-to-ROI analysis using regions with high predictive power in episodic memory or BSC: bilateral hippocampus (MNI coordinates, right: 27, -21, -15; left: -26,-22,-15), parahippocampus (MNI coordinates, right: 25, -18, -26; left: -23,-19,-25), and medial prefrontal cortex (mPFC, MNI coordinates, right: 7,45,-8; left -7,51,-7) and bilateral insula (MNI coordinates, right: 35, 18, 1; left: -33,16,1) as in Gauthier et al., 2020 (Gauthier et al., 2020). We also included the angular gyrus (MNI coordinates, right: 49, -57, 35; left: -44,-64,36) and precuneus (MNI coordinates, right: 9, -57, 35; left: -6,-58, 35) because both regions are reported both in memory and BSC studies (Bréchet et al., 2018; Cavanna et al., 2008; Lenggenhager et al., 2014; Tibon et al., 2019). We compared the functional connectivity between regions of the patient with the group of control participants acquired with ADNI (N = 23) using a multivariate approach to correct for multiple comparisons (Jafri et al., 2008).

4.4 Results

We built a neuropsychological profile of the patient and confirmed that she still had EAM deficit eight months after the diagnosis. We investigated how a difference of embodiment of a virtual avatar in different scenes would modulate the patient's episodic memory abilities. Experiment 1 used a visuomotor and perspectival mismatch to induce the disembodied condition. Experiment 2 used a different type of bodily mismatch where the patient encoded real-life scenes after induction of the FBI. In this manipulation, the patient viewed her back in front of her, while being stroked synchronously (embodied condition) or asynchronously (disembodied condition) with the projected image of herself. In both experiments, we tested her memory under free recall conditions and with specific questions targeting autonoetic consciousness and spatiotemporal content of the scenes. Finally, we compared the resting state functional connectivity of the patient with an age- and gender-matched control group, using an *apriori* network in an ROI-to-ROI analysis to explore the functional changes that occurred in the patient, potentially due to the hippocampal lesions.

Neuropsychological profile

We found that the patient had preserved episodic memory abilities as her score on the RVLT were not different from the norm (delayed recognition 9, total recognition 12, total trials 56). The patient was within normal range in the Trail Making test Part A (33 seconds , norm cut off: 81 seconds) and trail making test part B (79 seconds, norm cutoff: 299 seconds) indicating preserved psychomotor speed and mental flexibility. Her FAB score was at cutoff (16), indicating no executive dysfunction. Finally, her score in the autobiographical fluency test indicates an apparent deficit of EAM (**Table 1**). The patient had normal score of semantic information compared to the norm, but reduced number of personal episodic contents. The episodic events could not be recalled in full details. The patient was not able to mentally relive the events, but had only a feeling of familiarity. It is noteworthy that the patient could not recall events from her life which happened after 30 years old. The patient only guessed that these events were hers as she has been told so or seen herself in photography, but was not able to recollect any information. Together these results indicate that the patient had remaining EAM deficit at the time of our experiments. The deficit seemed to be specific for EAM with preserved semantic memory abilities.

Autobiographical fluency test	Life periods				
Life periods	0-17 years old	18-30 years	>30years old	last 5 years	last 12 months
Personal semantic information	23	11	12	10	4
Mean (SD) of subjects of the same age	*14.92(5.28)*	*12.83(9.67)*	*13.50 (5.38)*	*10.83 (3.78)*	*5.58 (4.64)*
Personal episodic	1*	5*	6	0***	2
Mean (SD) of subjects of the same age	*7.00 (3.13)*	*7.25 (1.76)*	*6.00 (1.95)*	*4.92 (2.02)*	*4.50 (2.07)*
R/K/G paradigm	K	K	G		R

Table 1. Summary results of the autobiographical fluency test. *The patient was below the norm for personal episodic content and within the norm for personal semantic information.*

Experiment 1

Visuomotor and perspectival mismatch was associated with better memory for visual perspective

First, we measured the sensitivity to the visuomotor and perspectival mismatch induced in half of the virtual scenes encoded. As with healthy controls, the patient was sensitive to the manipulation (**Figure 4A**), with higher sense of agency and body ownership in the embodied condition (visuomotor and perspectival congruency), compared to the disembodied condition (visuomotor and perspectival mismatch). Importantly, the questions controlling for experimental biases were low and not different between conditions, suggesting that the difference of sense of agency and sense of ownership captured between conditions was not due to suggestibility. These results show that the patient's condition did not impact her sensitivity to the bodily illusion induced experimentally and thus spared her sense of bodily self-consciousness.

We then investigated how the encoding in the different BSC state (embodied and disembodied) would affect the recollection of the virtual scene. We compared the autonoetic consciousness related to each scene by measuring autonoetic consciousness using the questionnaire presented in **Supplementary Table 1**. The patient could partially retrieve the first five scenes (3 encoded under embodied conditions), 3 of which only after receiving visual and sound cues. The overall autonoetic consciousness score of the five scenes was very low, with an average of 0.4 on normalized ratings (min=0, max=1). The fact that the scenes retrieved corresponded to the first five scenes suggested a strong effect of order in the recall session, probably due to tiredness. However, when asked to choose the perspective experienced at encoding over a choice of four pictures (**Figure 2**), the patient selected the correct view in three out four scenes encoded under disembodied conditions, and gave no correct answers for scenes in the embodied condition (**Figure 4B**).

*Figure 4. Successful induction of the bodily illusion and better recollection of the perspective under the disembodied condition in Experiment 1. **A.** The patient had a higher sense of agency and sense of ownership under visuomotor and perspectival congruency (embodied condition, red), compared to visuomotor and perspectival mismatch (disembodied condition, grey) as rated on a continuous scale between 0 and 1. **B.** The patient could recollect the perspective observed at encoding for three out of four scenes encoded under visuomotor and perspectival mismatch (disembodied condition, grey) but did not recollect any of the scenes encoded under visuomotor and perspectival congruency (embodied condition, red).*

Experiment 2

Visuotactile mismatch was associated with better memory for visual perspective

First, we measured the success of the FBI induced in Experiment 2. As classically obtained with control participants (Lenggenhager et al., 2007) the patient had a positive drift of perceived self-location towards the projected image of her back. The drift was more considerable under the visuotactile congruency condition (mean 24.25 cm, sd ± 13), as compared to the visuotactile mismatch condition (mean = 12 cm, ± 20; **Figure 5A**). These results suggest that similarly to Experiment 1, the patient was sensitive to our bodily illusion and embodied the observed back under visuotactile congruency.

Similarly to Experiment 1, for each scene encoded, one week after the encoding we presented the patient with four pictures of the scene taken from different points of view (**Figure 3B**). We found a similar trend as in Experiment 1, with three over four correct answers for the scenes encoded under the disembodied condition and one out of four correct answers for the scenes encoded in the embodied condition (**Figure 5B**).
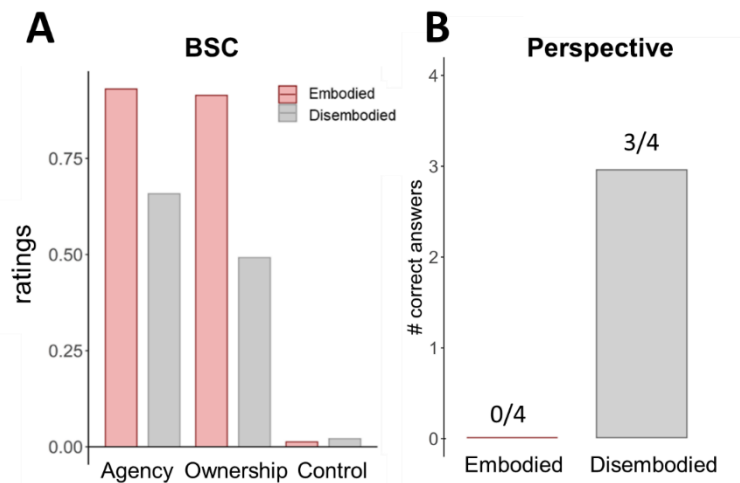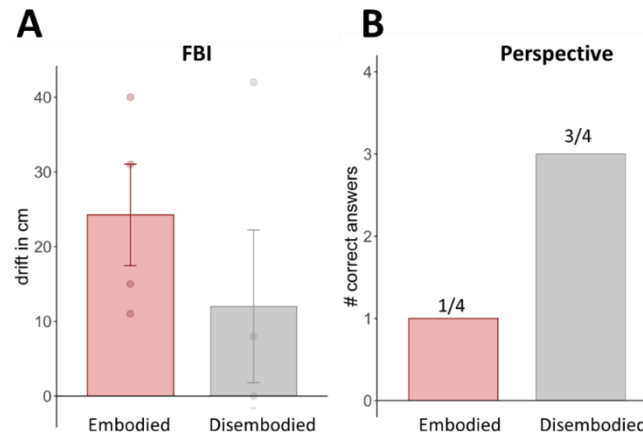
*Figure 5. Successful induction of the full-body illusion (FBI) and better recollection of the visual perspective under the disembodied condition in Experiment 2. **A.** The self-location drift induced by the FBI was larger under the visuotactile congruency (embodied condition, red). A positive drift indicates a perceived self-location biased towards the observed body's location. Dots indicate the drift at each trial, and bars indicate standard error of the mean. **B.** The patient could correctly recollect the visual perspective experienced at encoding for three out of four scenes encoded under visuotactile mismatch (disembodied condition, grey), and one scene encoded under visuotactile congruency (embodied condition).*

Embodied condition triggers more difficulty to recollect subjective details but not spatiotemporal information

In addition to the perspective task, one week after the encoding we measured the patient's autonoetic consciousness and tested her memory accuracy on the spatiotemporal context for each scene. The patient showed a higher autonoetic consciousness score when recollecting scenes from the disembodied condition (mean = 0.7, sd = ± 0.2, normalized scale) compared to the embodied condition (mean = 0.49, sd = ± 0.1) as depicted in **Figure 6A**. This difference seemed to be mainly triggered by the recollection of information related to the global experience (visual details, global level of detail, spatial context), as opposed to the reliving (global and emotional), which was rated very low for all scenes and did not differ between conditions.

We measured the patient memory accuracy by presenting her five two-alternative forced choice questions for each scene to test the retrieval of the spatiotemporal context ("what-where-when", as described in the method section). As depicted in **Table 2**, the patient could remember part of the information for each scene, and we did not find any difference between embodied and disembodied conditions (**Figure 6B**). However, the patient reported higher confidence on her answers for scenes encoded in the disembodied condition (mean = 0.93, sd = ± 0.4, normalized scale), as compared to scenes encoded in the embodied condition (mean = 0.68, sd ± 0.37; **Figure 6C**). This suggests that the subjective feeling of remembering was higher for scenes encoded under the disembodied condition, despite the absence of difference in memory accuracy. These results confirm and extend the findings of Experiment 1.

They indicate that a disembodied encoding of scenes improved the re-experience of the scenes and the subjective feeling of remembering (confidence).
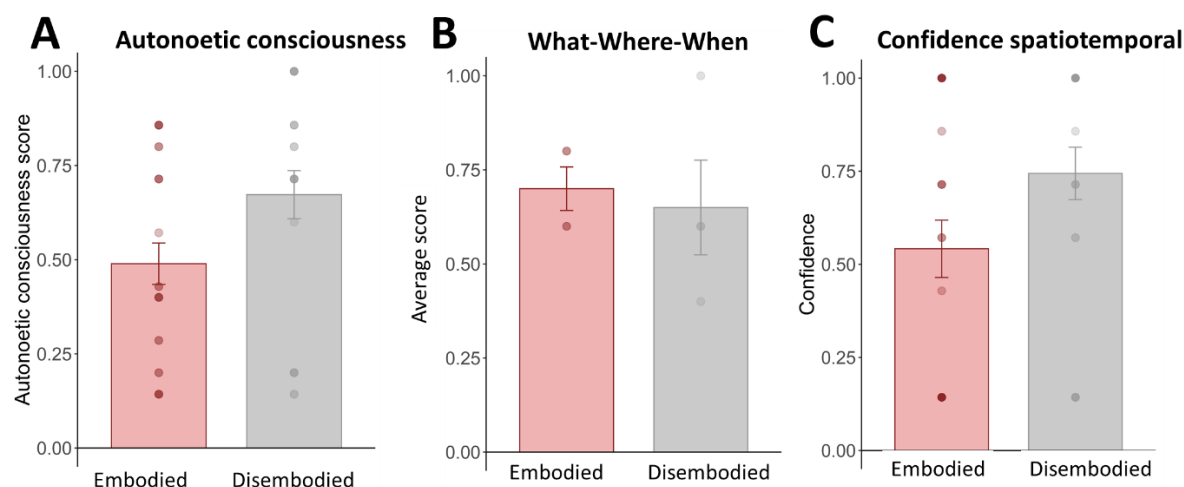
Figure 6. Disembodied condition lead to higher confidence and stronger autonoetic consciousness. A. *The patient had a higher level of recollection (autonoetic consciousness) in the disembodied condition (grey) compared to the embodied condition(red). Dots represent the normalized ratings for each question for each scene and bars indicate standard error of the mean. Autonoetic consciousness score was computed as the sum of the normalized ratings of the autonoetic consciousness questionnaire for each condition* ***B.*** *There was no difference between embodied (red) and disembodied (grey) conditions in retrieving the spatiotemporal context and content of each scene (What-Where-When). Dots represent the average score (number of correct answers) for each scene and bars indicate standard error of the mean.* ***C.*** *The patient was more confident in the What-Where-When answers associated with the disembodied condition (grey) compared to the embodied condition (red). Dots represent the normalized ratings for each question for each scene and bars indicate standard error of the mean.The confidence was computed as the average confidence ratings for each condition.*

Scene	Condition	Gender	Succeeded	Time	Visual field	Floor	Perspective
Printer	Embodied	1	1	0	1	0	0
Terrasse	Disembodied	1	0	1	0	1	0
Lab room	Embodied	0	1	1	0	1	0
Coffee machine	Disembodied	0	0	1	0	1	1
Auditorium	Embodied	1	0	1	1	1	0
Delivery dock	Disembodied	1	1	1	1	1	1
Library	Embodied	0	1	1	1	1	1
Reception	Disembodied	1	0	0	1	1	1

Table 2. Summary of the performance. *Performance (binary, correct=1, incorrect=0) for each of the five questions used to test memory related to the spatiotemporal information and content of each scene and for the question on the visual perspective.*

Scene	Conditions	Difficulty	Reliving E	Reliving G	Visual	Vividness	Location	Spatial	Relived	Rehearsal
Printer	Embodied	0.42	0.4	0.4	0.28	0.14	0.14	0.28	0	0
Terrasse	Disembodied	0.14	0.2	0.2	0.71	0.14	0.71	0.71	0	0
Lab room	Embodied	0.14	0.2	0.2	0.71	0.14	0.57	0.71	0	0.75
Coffee machine	Disembodied	0.85	0.6	0.8	1	0.85	1	0.85	0	0
Auditorium	Embodied	0.14	0.4	0.4	0.42	0.14	0.85	0.42	0	0
Delivery dock	Disembodied	0.14	0.2	0.2	0.71	0.14	0.71	0.71	0	0
Library	Embodied	0.85	0.8	0.8	0.71	0.85	0.85	0.85	0	0.25
Reception	Disembodied	1	0.8	1	0.85	1	1	1	1	0.75

Table 3. Summary of the strength of recollection as measured with the autonoetic consciousness questionnaire. Normalized ratings of the difficulty of remembering each scene and the autonoetic consciousness questionnaire to assess autonoetic consciousness for each scene, measured one week after encoding (Reliving E = reliving emotions, Reliving G = reliving global).

Resting state fMRI

ROI-to-ROI analysis

To better understand the neural correlates linked with the memory deficits of the patient, we performed an ROI-to-ROI analysis on the resting state functional connectivity of the patient. We used ROIs known to be involved in EAM or BSC (bilateral angular gyrus, precuneus, medial prefrontal cortex mPFC, parahippocampus, hippocampus, and insula). When compared to 23 age- and gender-matched healthy controls, the patient showed higher functional connectivity between the bilateral precuneus and the right mPFC ($F_{node}(2,21)$ = 9.92, p-FDR = 0.03; left precuneus and the right mPFC (T(22) = 3.32, p-FDR = 0.034; right precuneus and right mPFC (T(22) = 2.7, p-FDR = 0.035). We also found decreased functional connectivity between both hemisphere for the hippocampus and parahippocampus ($F_{node}(2,21)$ = 7.12, p-FDR = 0.033 ; left hippocampus versus right hippocampus :T(22) = -3.33, p-FDR = 0.029; left parahippocampus versus right parahippocampus T(22) = -3.59, p-FDR = 0.018). Additionally, decrease of functional connectivity between both precuneus was also observed ($F_{node}(1,22)$ = 8, p-FDR = 0.048 ,right versus left precuneus: T(22) = -2.84, p-FDR = 0.05). **Figure 7** summarizes the difference of functional connectivity observed in the patient. These results provide insight about which brain regions endured functional changes after the brain infection.
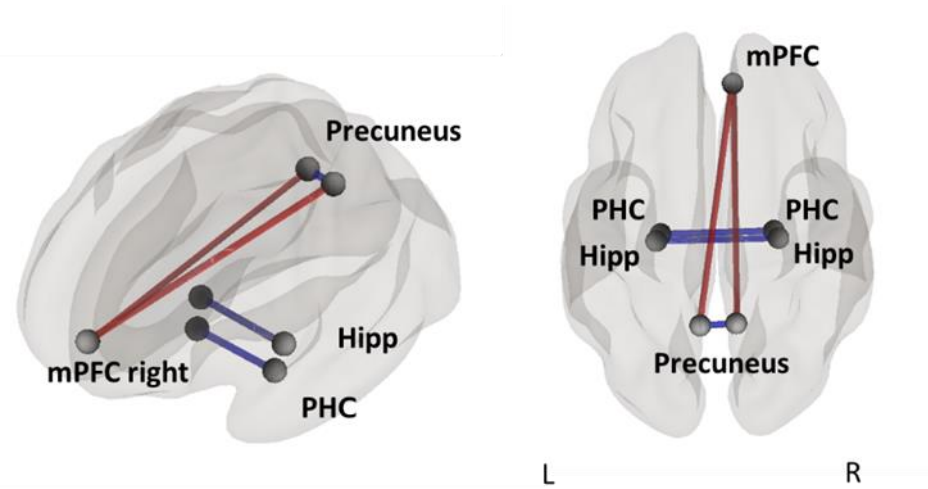
Figure 7: Functional connectivity difference between the patient and healthy control. *Resting-state functional connectivity differences between the patient and healthy female controls of the same age range (N = 23). Red connections indicate significantly higher functional connectivity and blue connection lower functional connectivity in the patient compared to the control group. Connections depicted on the figure were corrected for multiple comparison using a cluster threshold of p <0.05 with FDR-correction and a connection threshold of p <0.05. PHC = parahippocampus, mPFC = medial prefrontal cortex, Hipp = Hippocampus.*

4.5 Discussion

In this study, we had the opportunity to collaborate with an amnestic patient with a specific deficit of EAM due to lesions in the hippocampal complex. We used immersive VR and real-life like scenarios to better understand the impact of BSC on her deficits of EAM. We modulated the multisensory and sensorimotor integration of bodily signals to trigger different levels of involvement of the bodily self during the encoding of scenes. We hypothesized that preserved BSC, through the successful integration of bodily signals, would give rise to a higher bodily self component in the scene, thereby favoring the categorization of an event as being included in EAM. We tested the patient in two experiments in which she encoded half of the scenes under embodied conditions, with a successful multisensory and sensorimotor integration, hence a stable BSC. The remaining scenes were encoded under a disembodied condition, with disrupted multisensory and sensorimotor integration. We found that the patient was sensitive to the bodily manipulations induced and had more difficulties recollecting information encoded under the embodied condition. While the manipulation did not seem to affect memory accuracy for spatiotemporal context, autonoetic consciousness was worse in the embodied condition. Finally, we report increased resting state functional connectivity between the right mPFC and the bilateral precuneus and decreased functional connectivity between hemispheres in precuneus, parahippocampus and hippocampus in the patient, as compared to a group of age- and gender-matched controls. Together, these results suggest that manipulating BSC at encoding affects how memory is retrieved and links BSC with EAM.

The neuropsychological assessment of the patient confirmed that her amnesia was specific to EAM, as the amount of semantic personal details in the autobiographical fluency test was not significantly different from the normative range. In this patient, episodic memory deficits were accompanied by the inability to relive past episodes, i.e., a deficit in autonoetic consciousness (Markowitsch & Staniloiu, 2011; Tulving, 1985). The ability to consciously re-experience an event might be responsible, at least partly, for why EAM are so self-relevant and associated with self-consciousness processes (A. Gardiner et al., 2001; Markowitsch & Staniloiu, 2011; Prebble et al., 2013). Previous patient reports described conditions where EAM also lacked this self-component. One study reported the single case of a patient with a deficit in personal ownership of memories following a bike accident. The patient was able to recollect information from his past but could not attribute this memory to a personal experience (S. B. Klein & Nichols, 2012). Piolino and team reported the case of a patient with hypometabolism in the right ventral frontal lobe, leading to retrograde amnesia and to the inability to re-experience personal memories (Piolino et al., 2005), very similar to the patient reported in our study.

Studies manipulating sense of agency using visuomotor mismatch on healthy participants typically reported higher sense of agency under visuomotor congruency than visuomotor

mismatch (Imaizumi & Asai, 2015; Padilla-Castañeda et al., 2014). Consistently with studies on healthy participants, the patient had a stronger sense of agency and sense of ownership under visuomotor and perspectival congruency (embodied condition), suggesting that her lesions did not affect the multisensory and sensorimotor integration, nor the related subjective experience arising from it. We reproduced these findings in the second experiment in which the patient had a more considerable drift in self-location toward the observed body in the embodied condition, similar to what was reported in healthy participants (Lenggenhager et al., 2007). Previous single case studies showed that episodic memory deficits do not impair aspects of the cognitive self (Illman et al., 2011; Rathbone et al., 2009). Here, we add to this literature by showing that the bodily self can also be preserved, despite EAM deficits.

In the first experiment, the patient showed better recollection of the visual perspective adopted at encoding under the disembodied condition, compared to the embodied condition. We replicated this result in the second experiment for which we used a different sensory mismatch (visuotactile) to trigger the disembodied condition. Moreover, the confidence in the answers related to memory accuracy, and the strength of autonoetic consciousness were also lower in the embodied condition (Experiment 2), although no difference was observed for memory accuracy. Dissociation between memory accuracy and autonoetic consciousness has been reported in previous studies (Rubin et al., 2003; Scoboria et al., 2015; Scoboria & Pascal, 2016). This phenomenon is also widely reported in the study of the impact of emotions on EAM (Kensinger & Ford, 2020; Phelps & Sharot, 2008; Rimmele et al., 2011), where increased emotional re-experience is not necessarily linked with better memory accuracy. The lower autonoetic consciousness and overall episodic memory recollection under the embodied condition suggest that the embodied condition led to more difficulties in recollecting information, mimicking her deficits in recollecting self-related episodes. These findings are at odds with the few studies investigating BSC and EAM in healthy participants, in which the embodied condition triggers an enhanced recollection of subjective aspects (emotions, reliving, vividness) compared to the disembodied condition (Bergouignan et al., 2014; Iriye & Ehrsson, 2022). Therefore, we propose that the bilateral lesions in the hippocampal complex affect the association of BSC with EAM.

This was further supported by a decreased functional connectivity at rest between the bilateral hippocampus and the bilateral parahippocampus when we compared the patient with aged- and gender- matched control. Consistent with the MTT theory which states that the hippocampus remains central to the retrieval of EAM (Moscovitch et al., 2016; Sekeres et al., 2017, 2018), this reduced functional connectivity at rest could explain in part the EAM deficit of the patient. We intend in the future to acquire a structural scan of the patient's lesions with a high resolution (7T MRI), to better understand which part of the lesioned hippocampal complex could be responsible for the EAM deficit of the patient. We also observed increased functional connectivity between the right mPFC and bilateral precuneus when compared to control. The prefrontal cortex is a key region in episodic memory (Preston & Eichenbaum, 2013; Simons & Spiers, 2003) connected with the anterior part of the

hippocampus (Preston & Eichenbaum, 2013). Decreased resting-state functional connectivity between prefrontal cortex and parietal regions has been linked to attentional deficit in patients with temporal lobe epilepsy (Ives-Deliperi & Butler, 2021). In light of this description, we could interpret this increase of functional connectivity as compensatory mechanism to enhance attention.

Additionally, the difference of autonoetic consciousness between the embodied and disembodied condition could indicate the use of different neural substrate to retrieve information encoded under different BSC states. Although purely speculative, as we did not record the brain activity during the retrieval of EAM in this study, the use of different brain regions for different type of recollection has been demonstrated. The functional connectivity between parahippocampus and hippocampus has been linked to autobiographical memory recollection. In contrast, the functional connectivity of the middle temporal gyrus with the temporal pole has been associated with the retrieval of public events and general knowledge (Maguire et al., 2000).

To conclude, we reported the rare case of an amnestic patient suffering from EAM deficit following a fungal brain infection. Similarly to other single cases reported in the literature, her deficit was specific to the episodic component of autobiographical memory. We showed that the patient had more difficulties recollecting information encoded under conditions where the bodily self was not altered. This suggests that BSC is part of the mechanism involved in EAM recollection, severely impaired in this patient. Altogether, this study showed that encoding an episode under a disembodied condition leads to better memory in this patient, by potentially bypassing the altered memory circuits that associate the memory with the bodily self. This single case report brings new evidence towards the role of BSC in EAM recollection.

4.6 References

Wilson, B. A., Cockburn, J., & Baddeley, A. (2008). *The Rivermead behavioural memory test*. Pearson.Bergouignan, L., Nyberg, L., &
   Ehrsson, H. H. (2014). Out-of-body–induced hippocampal amnesia. *Proceedings of the National Academy of Sciences*, *111*(12),
   4421-4426. https://doi.org/10.1073/pnas.1318801111

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature Reviews Neuroscience*, *13*(8), Art. 8.
   https://doi.org/10.1038/nrn3292

Blanke, O., & Castillo, V. (Éds.). (2007). Clinical neuroimaging in epileptic patients with autoscopic hallucinations and out-of-body
   experiences. *Epileptologie*.

Blanke, O., & Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. *Trends in Cognitive Sciences*, *13*(1), 7-13.
   https://doi.org/10.1016/j.tics.2008.10.003

Blanke, O., & Mohr, C. (2005). Out-of-body experience, heautoscopy, and autoscopic hallucination of neurological origin : Implications for
   neurocognitive mechanisms of corporeal awareness and self-consciousness. *Brain Research Reviews*, *50*(1), 184-199.
   https://doi.org/10.1016/j.brainresrev.2005.05.008

Blanke, O., Slater, M., & Serino, A. (2015). Behavioral, Neural, and Computational Principles of Bodily Self-Consciousness. *Neuron*, *88*(1),
   145-166. https://doi.org/10.1016/j.neuron.2015.09.029

Bréchet, L., Grivaz, P., Gauthier, B., & Blanke, O. (2018). Common Recruitment of Angular Gyrus in Episodic Autobiographical Memory
   and Bodily Self-Consciousness. *Frontiers in Behavioral Neuroscience*, *12*.
   https://www.frontiersin.org/articles/10.3389/fnbeh.2018.00270

Bréchet, L., Mange, R., Herbelin, B., Theillaud, Q., Gauthier, B., Serino, A., & Blanke, O. (2019). First-person view of one's body in
   immersive virtual reality : Influence on episodic memory. *PLOS ONE*, *14*(3), e0197763.
   https://doi.org/10.1371/journal.pone.0197763

Brodt, S., Gais, S., Beck, J., Erb, M., Scheffler, K., & Schönauer, M. (2018). Fast track to the neocortex : A memory engram in the posterior
   parietal cortex. *Science*, *362*(6418), 1045-1048. https://doi.org/10.1126/science.aau2528

Cavanna et al.,. (2008). *Chapter 3.7 The role of the precuneus in episodic memory—ScienceDirect*.
   https://www.sciencedirect.com/science/article/abs/pii/S1569733908002208

Dalla Barba, G., Brazzarola, M., Barbera, C., Marangoni, S., Causin, F., Bartolomeo, P., & Thiebaut de Schotten, M. (2018). Different
   patterns of confabulation in left visuo-spatial neglect. *Experimental Brain Research*, *236*(7), 2037-2046.
   https://doi.org/10.1007/s00221-018-5281-8

De Renzi, E., Lucchelli, F., Muggia, S., & Spinnler, H. (1997). Is memory loss without anatomical damage tantamount to a psychogenic
   deficit? The case of pure retrograde amnesia. *Neuropsychologia*, *35*(6), 781-794. https://doi.org/10.1016/S0028-3932(97)00018-3

Dritschel, B. H., Williams, J. M. G., Baddeley, A. D., & Nimmo-Smith, I. (1992). Autobiographical fluency : A method for the study of
   personal memory. *Memory & Cognition*, *20*(2), 133-140. https://doi.org/10.3758/BF03197162

Dubois, B., Slachevsky, A., Litvan, I., & Pillon, B. (2000). The FAB : A Frontal Assessment Battery at bedside. *Neurology*, *55*(11),
   1621-1626.

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

Gardiner, J. M., Ramponi, C., & Richardson-Klavehn, A. (1998). Experiences of Remembering, Knowing, and Guessing. *Consciousness and Cognition*, *7*(1), 1-26. https://doi.org/10.1006/ccog.1997.0321

Gauthier, B., Bréchet, L., Lance, F., Mange, R., Herbelin, B., Faivre, N., Bolton, T. A. W., Ville, D. V. D., & Blanke, O. (2020). First-person body view modulates the neural substrates of episodic memory and autonoetic consciousness : A functional connectivity study. *NeuroImage*, *223*, 117370. https://doi.org/10.1016/j.neuroimage.2020.117370

Gomez, A., Rousset, S., & Charnallet, A. (2012). Spatial deficits in an amnesic patient with hippocampal damage : Questioning the multiple trace theory. *Hippocampus*, *22*(6), 1313-1324. https://doi.org/10.1002/hipo.20968

Holland, S. M., & Smulders, T. V. (2011). Do humans use episodic memory to solve a What-Where-When memory task? *Animal Cognition*, *14*(1), 95-102. https://doi.org/10.1007/s10071-010-0346-5

Illman, N. A., Rathbone, C. J., Kemp, S., & Moulin, C. J. A. (2011). Autobiographical memory and the self in a case of transient epileptic amnesia. *Epilepsy & Behavior*, *21*(1), 36-41. https://doi.org/10.1016/j.yebeh.2011.02.022

Imaizumi, S., & Asai, T. (2015). Dissociation of agency and body ownership following visuomotor temporal recalibration. *Frontiers in Integrative Neuroscience*, *9*. https://www.frontiersin.org/articles/10.3389/fnint.2015.00035

Iriye, H., & Ehrsson, H. H. (2022). Perceptual illusion of body-ownership within an immersive realistic environment enhances memory accuracy and re-experiencing. *IScience*, *25*(1), 103584. https://doi.org/10.1016/j.isci.2021.103584

Ives-Deliperi, V., & Butler, J. T. (2021). Mechanisms of cognitive impairment in temporal lobe epilepsy : A systematic review of resting-state functional connectivity studies. *Epilepsy & Behavior*, *115*, 107686. https://doi.org/10.1016/j.yebeh.2020.107686

Jafri et al. (2008). *A method for functional network connectivity among spatially independent resting-state components in schizophrenia—ScienceDirect*. https://www.sciencedirect.com/science/article/pii/S1053811907010282

Jeannerod, M. (2009). The sense of agency and its disturbances in schizophrenia : A reappraisal. *Experimental Brain Research*, *192*(3), 527-532. https://doi.org/10.1007/s00221-008-1533-3

Kapur N. Ellison, D., Smith, M. P., McLellan, D. L., & Burrows, E. H. (1992). FOCAL RETROGRADE AMNESIA FOLLOWING BILATERAL TEMPORAL LOBE PATHOLOGY : A NEUROPSYCHOLOGICAL AND MAGNETIC RESONANCE STUDY. *Brain*, *115*(1), 73-85. https://doi.org/10.1093/brain/115.1.73

Kensinger, E. A., & Ford, J. H. (2020). Retrieval of Emotional Events from Memory. *Annual Review of Psychology*, *71*(1), 251-272. https://doi.org/10.1146/annurev-psych-010419-051123

Klein, S. B., & Nichols, S. (2012). Memory and the Sense of Personal Identity. *Mind*, *121*(483), 677-702. https://doi.org/10.1093/mind/fzs080

Lavenex, P., & Amaral, D. G. (2000). Hippocampal-neocortical interaction : A hierarchy of associativity. *Hippocampus*, *10*(4), 420-430. https://doi.org/10.1002/1098-1063(2000)10:4<420::AID-HIPO8>3.0.CO;2-5

Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video Ergo Sum : Manipulating Bodily Self-Consciousness. *Science*, *317*(5841), 1096-1099. https://doi.org/10.1126/science.1143439

Lenggenhager et al.,. (2014). *The bodily self and its disorders : Neurological, psychologic... : Current Opinion in Neurology*. https://journals.lww.com/co-neurology/fulltext/2014/12000/the_bodily_self_and_its_disorders___neurological,.6.aspx

Levine, B., Black, S. E., Cabeza, R., Sinden, M., Mcintosh, A. R., Toth, J. P., Tulving, E., & Stuss, D. T. (1998). Episodic memory and the self in a case of isolated retrograde amnesia. *Brain*, *121*(10), 1951-1973. https://doi.org/10.1093/brain/121.10.1951

Levine, B., Svoboda, E., Turner, G. R., Mandic, M., & Mackey, A. (2009). Behavioral and functional neuroanatomical correlates of anterograde autobiographical memory in isolated retrograde amnesic patient M.L. *Neuropsychologia*, *47*(11), 2188-2196. https://doi.org/10.1016/j.neuropsychologia.2008.12.026

Maeda, T., Takahata, K., Muramatsu, T., Okimura, T., Koreki, A., Iwashita, S., Mimura, M., & Kato, M. (2013). Reduced sense of agency in chronic schizophrenia with predominant negative symptoms. *Psychiatry Research*, *209*(3), 386-392. https://doi.org/10.1016/j.psychres.2013.04.017

Maguire, E. A., Mummery, C. J., & Büchel, C. (2000). Patterns of hippocampal-cortical interaction dissociate temporal lobe memory subsystems. *Hippocampus*, *10*(4), 475-482. https://doi.org/10.1002/1098-1063(2000)10:4<475::AID-HIPO14>3.0.CO;2-X

Markowitsch, H. J., & Staniloiu, A. (2011). Memory, autonoetic consciousness, and the self. *Consciousness and Cognition*, *20*(1), 16-39. https://doi.org/10.1016/j.concog.2010.09.005

Mayes, A. R., Isaac, C. L., Holdstock, J. S., Cariga, P., Gummer, A., & Roberts, N. (2003). Long-Term Amnesia : A Review and Detailed Illustrative Case Study. *Cortex*, *39*(4), 567-603. https://doi.org/10.1016/S0010-9452(08)70855-4

Moore, K., Convery, R., Bocchetta, M., Neason, M., Cash, D. M., Greaves, C., Russell, L. L., Clarke, M. T. M., Peakman, G., van Swieten, J., Jiskoot, L., Moreno, F., Barandiaran, M., Sanchez-Valle, R., Borroni, B., Laforce, R., Doré, M.-C., Masellis, M., Tartaglia, M. C., … Rohrer, J. D. (2022). A modified Camel and Cactus Test detects presymptomatic semantic impairment in genetic frontotemporal dementia within the GENFI cohort. *Applied Neuropsychology: Adult*, *29*(1), 112-119. https://doi.org/10.1080/23279095.2020.1716357

Moscovitch, M., Cabeza, R., Winocur, G., & Nadel, L. (2016). Episodic Memory and Beyond : The Hippocampus and Neocortex in Transformation. *Annual review of psychology*, *67*, 105-134. https://doi.org/10.1146/annurev-psych-113011-143733

Nieto-Castanon, A. (2020). *Handbook of functional connectivity Magnetic Resonance Imaging methods in CONN*. Hilbert Press.

Padilla-Castañeda, M. A., Frisoli, A., Pabon, S., & Bergamasco, M. (2014). The Modulation of Ownership and Agency in the Virtual Hand Illusion under Visuotactile and Visuomotor Sensory Feedback. *Presence*, *23*(2), 209-225. https://doi.org/10.1162/PRES_a_00181

Phelps, E. A., & Sharot, T. (2008). How (and Why) Emotion Enhances the Subjective Sense of Recollection. *Current Directions in Psychological Science*, *17*(2), 147-152. https://doi.org/10.1111/j.1467-8721.2008.00565.x

Piolino, P., Hannequin, D., Desgranges, B., Girard, C., Beaunieux, H., Giffard, B., Lebreton, K., & Eustache, F. (2005). Right ventral frontal hypometabolism and abnormal sense of self in a case of disproportionate retrograde amnesia. *Cognitive Neuropsychology*, *22*(8), 1005-1034. https://doi.org/10.1080/02643290442000428

Prebble, S. C., Addis, D. R., & Tippett, L. J. (2013). Autobiographical memory and sense of self. *Psychological Bulletin*, *139*, 815-840. https://doi.org/10.1037/a0030146

Preston, A. R., & Eichenbaum, H. (2013). Interplay of Hippocampus and Prefrontal Cortex in Memory. *Current Biology*, *23*(17), R764-R773. https://doi.org/10.1016/j.cub.2013.05.041

Puel, M., Bezy-Vié, C., Busigny, T., Cazaux, P., Arrabie, L., Basaglia-Pappas, S., Barbeau, E. J., Pariente, J., & Thomas-Anterion, C. (2016). Gretop Visages et Gretop Noms : Mémoire des personnes célèbres, un outil d'aide au diagnostic précoce dans les pathologies neurodégénératives. *Revue de neuropsychologie*, *8*(3), 201-214. https://doi.org/10.3917/rne.083.0201

Rathbone, C. J., Moulin, C. J. A., & Conway, M. A. (2009). Autobiographical memory and amnesia : Using conceptual knowledge to ground the self. *Neurocase*, *15*(5), 405-418. https://doi.org/10.1080/13554790902849164

Reitan, R. M., & Wolfson, D. (1985). *The Halstead-Reitan Neuropsychological Test Battery : Theory and Clinical Interpretation*. Neuropsychology Press.

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Rimmele, U., Davachi, L., Petrov, R., Dougal, S., & Phelps, E. A. (2011). Emotion enhances the subjective feeling of remembering, despite lower accuracy for contextual details. *Emotion*, *11*, 553-562. https://doi.org/10.1037/a0024246

Robin, J., & Moscovitch, M. (2017). Details, gist and schema : Hippocampal–neocortical interactions underlying recent and remote episodic and spatial memory. *Current Opinion in Behavioral Sciences*, *17*, 114-123. https://doi.org/10.1016/j.cobeha.2017.07.016

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

Scoboria, A., & Pascal, L. (2016). Dissociating appraisals of accuracy and recollection in autobiographical remembering. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *42*, 1068-1077. https://doi.org/10.1037/xlm0000230

Scoboria, A., Talarico, J. M., & Pascal, L. (2015). Metamemory appraisals in autobiographical event recall. *Cognition*, *136*, 337-349. https://doi.org/10.1016/j.cognition.2014.11.028

Sekeres, M. J., Moscovitch, M., & Winocur, G. (2017). Mechanisms of Memory Consolidation and Transformation. In N. Axmacher & B. Rasch (Éds.), *Cognitive Neuroscience of Memory Consolidation* (p. 17-44). Springer International Publishing. https://doi.org/10.1007/978-3-319-45066-7_2

Sekeres, M. J., Winocur, G., & Moscovitch, M. (2018). The hippocampus and related neocortical structures in memory transformation. *Neuroscience Letters*, *680*, 39-53. https://doi.org/10.1016/j.neulet.2018.05.006

Tibon, R., Fuhrmann, D., Levy, D. A., Simons, J. S., & Henson, R. N. (2019). Multimodal Integration and Vividness in the Angular Gyrus During Episodic Encoding and Retrieval. *Journal of Neuroscience*, *39*(22), 4365-4374. https://doi.org/10.1523/JNEUROSCI.2102-18.2018

Tsakiris, M., Hesse, M. D., Boy, C., Haggard, P., & Fink, G. R. (2007). Neural Signatures of Body Ownership : A Sensory Network for Bodily Self-Consciousness. *Cerebral Cortex*, *17*(10), 2235-2244. https://doi.org/10.1093/cercor/bhl131

Tulving, E. (1985). Memory and consciousness. *Canadian Psychology / Psychologie canadienne*, *26*, 1-12. https://doi.org/10.1037/h0080017

Tulving, E. (2002). Episodic memory : From mind to brain. *Annual Review of Psychology*, *53*, 1-25. https://doi.org/10.1146/annurev.psych.53.100901.135114

WANG, Q., & CONWAY, M. A. (2006). Autobiographical Memory, Self, and Culture. In *Memory and Society*. Psychology Press.

Wechsler, D. (2008). *Wechsler Adult Intelligence Scale—Fourth Edition*. https://doi.org/10.1037/t15169-000

4.7 Supplementary Information

Text

Rey Auditory Verbal Learning Test

The Rey Auditory Verbal Learning Test (RAVLT; Rey, 1941) is a neuropsychological assessment designed to evaluate verbal episodic memory in patients. It is used to evaluate the nature and severity of memory impairment and to evaluate changes in memory function or processes (encoding-storage-retrieval) over time. It is presented as a list-learning test in which the examiner says aloud to the patient a list of 15 words, 1 second per word. The patient is asked to listen carefully and to recall as many words as possible from the list, and in any order. After five repetitions of free-recall during which the 15 words are read aloud again, a second "interference" list (List B) is presented in the same manner, and the patient is asked to recall as many words from List B as possible. After the interference trial, the patient is immediately instructed to recall the words from List A, which she/he heard five times previously. After a delay of 20 minutes (delayed recall), the patient is invited to recall freely again the words from List A. After this delayed recall, a recognition task is administered. A list of 50 words is presented and read aloud to the patient. This list contains all of the words from Lists A and B, and 20 other phonemically and/or semantically similar words. The five recall trials and the delayed recall of List A can be represented as a learning curve, indicating relative memory capacity. Furthermore, the correct number of recalled words from List A, the number of intrusions and perseverative errors are assessed.

Frontal assessment battery

The Frontal Assessment Battery (Dubois et al., 2000) is a short and brief neuropsychological test assessing the presence and severity of a dysexecutive syndrome affecting both cognition and motor behaviour. Six components of executive functions are measured:
1). Abstract reasoning (conceptualisation)
2). Initiation and mental flexibility
3). Motor programming
4). Sensitivity to interference
5). Inhibitory control/self-monitoring
6). Environmental autonomy (dependency to sensory stimuli).
A score less than 15/18 (with less than 5 years of schooling) and less than 16/18 (with more than 10 years of schooling) is considered pathological.

TMT A and B

The Trail Making Test (Reitan & Wolfson, 1985) is a test during which the execution of the task is timed. Part A explores perceptual-motor speed (visuomotor tracking) while part B requires more psychomotor speed, mental flexibility and working memory. Part A consists of 25 circles,

numbered from 1 to 25 arranged in a specific geometric pattern. The patient is given a pen and is instructed to draw a continuous line to connect each circle in ascending order as fast and accurately as possible. Part B also consists of 25 circles in which there are numbers (1 to 12) and letters (A to L). The patient is asked to connect the circles this time alternating numbers and letters. In other words, the "trail" would be connected starting with number 1, then letter A. The alternating connexion follows the numbers in ascending order, and the letter in alphabetical order like follows: 1-A-2-B-3-C etc. The time taken (in seconds) to complete each part is evaluated as well as the number of self-corrected and non-self corrected errors.

Autobiographical fluency test

The Autobiographical fluency test (Dritschel et al., 1992) was designed to assess the ability to recall autobiographical episodes (e.g., my first day at university, my bicycle accident) and personal facts (or autobiographical personal semantic information) such as names of friends and teachers, from different lifetime periods (0-17 years old, 18-30 years, 30 years old-before last 5 years, last 5 years, last 12 months). The patient is given 90 seconds to retrieve as many items as possible for each type of autobiographical information and for each life period. The number of episodes and personal semantic information are calculated per life period and compared to normative data from a sample of healthy subjects of the same age group and level of schooling.

Additionally, the Remember/Know/Guess paradigm (J. M. Gardiner et al., 1998; Tulving, 2002) was applied to evaluate autonoetic consciousness associated with each recalled autobiographical episode (not applicable for personal semantic information). "Remember" responses correspond to the conscious recollection (reliving of the original event) of vivid contextual, sensory, perceptual and/or emotional details of the event such as "what" happened, "when" and "where" the event occurred. "Know" responses correspond to the feeling of familiarity towards the event without being able to recollect the contextual details of the episode. "Guess" responses indicate no memory of the episode whereby the patient is only guessing its occurrence.

Table & Figure

Statement	Scale	Reference	# Index
My memory for this event involves sound	1-7 little/A lot	MCQ	1
My memory for this event involves smell	1-7 little/A lot	MCQ	2
My memory for this event involves touch	1-7 little/A lot	MCQ	3
The overall tone of the memory is	Negative/Neutral/Positive	MCQ	4
In this event I was	An observer /A participant	MCQ	5
I remember the event through my own eyes as during the event	1-7 Not at all/Definitely	MCQ	6

When you picture this event do you visualize it as a continuous video that plays with break, moving video clips with some breaks, one moving image or is it more like a set of snapshot with no movement, or something else?	1-7 One smooth video/video clips with breaks/one moving image/snapshot in sequence/one static snapshot/Hazy image/no image	EAMI	7
How often would you estimate you have thought about this memory since it first occurred?	1- 4 Frequently/Occasionnaly/Rarely/Never Never/Rarely/Occasionnaly/Frequently	EAMI	8
How often would you estimate you have spoken about this memory since it first occurred?	1-4 Frequently/Occasionnaly/Rarely/Never Never/Rarely/Occasionnaly/Frequently	EAMI	9
When you recall this event are you viewing the scene through your « own eyes » or can you see yourself in the memory from a third-person perspective?	Own eyes/Mixture/Third person/something different/no imagery	EAMI	10
When you recall this event how would you describe it in terms of vividness? This can apply to the richness of sights, sounds, smells, tastes, touch, and any movements you may have made.	1-7 very vivid/very vague 1-7 very vague/very vivid	EAMI	11
The relative spatial arrangement of people in my memory for the event is	1-7 Vague/Distinct	MCQ	12
My memory for the time when the event takes place is	1-7 Vague/Distinct	MCQ	13
When I remember the event, I see myself entirely in the scene as if I was watching a movie	1-7 Not at all/Definitely	MCQ	14
When I think about or tell this memory, I feel like I relive it as it happened	1-7 Not at all/Definitely	MCQ	15
I remember the movements and gestures I made with my body at the time of the event	1-7 / Vague/Distinct	In-house	16
My memory for this event is	1-7 Dim/Clear	MCQ	17
My memory for this event involves visual details	1-7 Little/ A lot	MCQ	18
My memory for this event is	1-7 Sketchy/very detailed	MCQ	19
My memory for the location where the event takes place is	1-7 Vague/Distinct	MCQ	20
Relative spatial arrangement of objects in my memory for the event is	1-7 Vague/Distinct	MCQ	21
When you think about this event now, do you re-experience any of the emotion you originally felt at the time? To what extent are you re-experiencing this emotion as a percentage?	0/25/50/75/100%	EAMI	22
To what extent are you re-experiencing this memory as a percentage?	0/25/50/75/100%	EAMI	23
Would you say you are reliving this memory or looking back on it?	Reliving/Looking back	EAMI	24
I remember how I felt at the time when the event took place	1-7 Not at all/Definitely	MCQ	25
I remember what I thought at the time	1-7 Not at all/Definitely	MCQ	26

Supplementary Table 1. Questionnaire items to test the patient's autonoetic consciousness. *The full questionnaire was used for Experiment 1. We used items 17-24 for Experiment 2. Scale from original questionnaire is indicated in black, new scale is indicated in green.*

Supplementary Figure 1. Eight scenes encoded in Experiment 2. *The patient encoded eight scenes in eight different location, with different actor and scenario (library, coffee machine, printer, reception, delivery dock, auditorium, terrasse, and lab room).*

Scene	Conditions	Gender	Succeeded	Morning	VisualField	Floor	Perspective
Printer	Embodied	0.14	0.43	0.72	1	0.14	0.14
Terrasse	Disembodied	0.14	0.14	1	0.86	1	0.143
Lab room	Embodied	0.143	0.143	0.86	0.57	0.143	0.14
Coffee Machine	Disembodied	0.7	1	1	0.57	1	1
Auditorium	Embodied	0.143	0.71	1	0.71	0.14	0.14
Delivery Dock	Disembodied	1	0.14	1	0.57	1	0.14
Library	Embodied	0.57	1	1	1	1	1
Reception	Disembodied	1	1	0.71	1	1	0.71

Supplementary Table 2. *Summary of the normalized confidence for each of the five questions used to test memory related to the spatiotemporal information and content of each scene and for the question on the visual perspective.*

5. Study 4: Investigating sensorimotor alteration of bodily self-consciousness and its impact on episodic memory in stroke population: A proof of concept study

Authors

Nathalie Heidi Meyer[1], Baptiste Gauthier [2], Jevita Potheegadoo[1], Florian Lance[1], Martino Ceroni[3], Lisa Fleury[3], Julia Brügger[3], Andeol Cadic[3], Sara Stampaccia[1], Friedhelm Hummel[3], Olaf Blanke [1, 4]

Affiliations

[1] Laboratory of Cognitive Neuroscience, Neuro-X Institute & Brain Mind Institute and Center for Neuroprosthetics, Faculty of Life Sciences, Ecole Polytechnique Fédérale de Lausanne, Geneva, Switzerland

[2] Clinical Research Unit, Neuchâtel Hospital Network, 2000 Neuchâtel, Switzerland

[3] UPHUMMEL lab, Neuro-X Institute & Brain Mind Institute and Center for Neuroprosthetics, Faculty of Life Sciences, Ecole Polytechnique Fédérale de Lausanne, Geneva, Switzerland

[4] Department of Clinical Neurosciences, University Hospital Geneva, Rue Micheli-du-Crest 24, 1205, Geneva Switzerland

5.1 Abstract

Episodic memory, the conscious recollection of sensory information and subjective mental state from one's own past, heavily relies on the multisensory and sensorimotor integration of external stimuli experienced during an event. Interestingly, the subjective experience of a unitary self, bodily self-consciousness (BSC) also arises from the multisensory and sensorimotor integration of bodily signals. Recent studies have thus proposed that these two processes are tightly linked together. If BSC is associated with episodic memory, then clinical population with alteration of sensorimotor integration should show altered BSC and reduced recollection abilities. In this proof-of-concept study, we tested this hypothesis in a population of chronic stroke patients with upper limb motor impairment at stroke onset. We designed immersive virtual reality scenarios and manipulated BSC to investigate whether changes of sensorimotor integration led to changes of episodic memory retrieval. We report difference of sensitivity to BSC manipulation and suggest that this difference is due to alteration of BSC processes in some of the stroke patients. Furthermore, the autonoetic consciousness of events encoded after the stroke onset was higher than the strength for events encoded before the stroke onset. Together these results indicate that stroke patient population could provide important information to better understand the neural substrate linking BSC with episodic memory.

5.2 Introduction

Our ability to remember our past is an important feature of human cognition. Autobiographical memory is defined as the collection of personal past events and contributes to the maintenance of our self-identity in time (Conway, 2001; Prebble et al., 2013; Wang & Conway, 2006). Episodic memory provides information about our past on personally relevant events in a unique spatiotemporal context. Episodic memory are associated with the recall of rich sensory and perceptual details (Markowitsch & Staniloiu, 2011; Piolino et al., 2006; Tulving, 1985). The re-experience and recollection of these details are enabled by autonoetic consciousness, our ability to mentally project oneself in the past and recollect the subjective experience linked to an event (Markowitsch & Staniloiu, 2011; Piolino et al., 2006; Tulving, 1985).

At the neural level, episodic memory retrieval is associated with cortical activation of sensory regions involved at encoding (Boccia et al., 2019; Bosch et al., 2014; Wheeler, 2000). Some studies proposed that the sensory signals are integrated in the cortex, and later reactivated by the hippocampus during episodic memory retrieval (Moscovitch et al., 2005; Nadel et al., 2000; Ryan et al., 2001). Interestingly, bodily self-consciousness (BSC) the experience of a unitary self within the body boundaries is also generated from the multisensory and sensorimotor integration of bodily signals (Blanke, 2012; Blanke et al., 2015; Tsakiris et al., 2007). More specifically, BSC arises from four different subjective experiences creating this feeling of a unitary self. These four building blocks are the following: the experience of the sense of agency (SoA) , the feeling of being in control of once own body and its related action, the sense of ownership, the feeling that the body belongs to one self, the first-person perspective (1PP), the view of the world from one's own body, and the sense of self-location (the feeling that oneself is located "inside" the body (Blanke et al., 2015; Tsakiris et al., 2010). At the neural level, BSC substrate depends on a large range of cortical areas such as the premotor cortex (PMC), supplementary area (SMA), insula, and posterior parietal regions (Park & Blanke, 2019).

Based on their shared dependencies of multisensory and sensorimotor integration, recent studies suggest that BSC and episodic memory processes are associated. The primary empirical evidence showed that a change from a 1PP to the third-person perspective (3PP) or an absence of body view at encoding or retrieval, leads to a reduced episodic memory (Bergouignan, 2021; Bergouignan et al., 2014; Bréchet et al., 2019; Gauthier et al., 2020; Iriye & St. Jacques, 2021). Recently, one study showed that this association was not specific to 1PP as a reduction of sense of ownership lead to reduced emotional reliving and vividness of episodic memory (Iriye & Ehrsson, 2022). Although these studies provide empirical evidence linking BSC and episodic memory, less is known about the neural mechanism underlying such association.

Since both BSC and episodic memory rely on successful multisensory and sensorimotor integration, clinical populations with impaired multisensory or sensorimotor integration should show episodic memory deficits. Such deficit has been observed in schizophrenic patients and related to altered sensorimotor integration (Jeannerod, 2009; Ricarte et al., 2017). The stroke population is another clinical cohort in which sensorimotor integration is altered depending on the lesion location (Baumgartner et al., 2018; Meer et al., 2010). However, episodic memory is not systematically investigated in stroke patients and studies reporting episodic memory deficit in stroke patients usually do not focus specifically on patients with sensorimotor impairment (Lim & Alexander, 2009). In this proof-of-concept study, we used immersive virtual reality (VR) to assess both BSC and episodic memory in stroke patients with sensorimotor impairment after stroke onset. We hypothesized that stroke patients with motor impairment should show reduced BSC-related subjective experience and hence reduced episodic memory. First, we investigated whether a BSC manipulation during the encoding of virtual scene led to difference in recognition performance of patients. We then investigated whether autonoetic consciousness was different for memory encoded before compared to after stroke onset.

5.3 Methods

Patients

Seven chronic stroke patients (4 males; 5 left hemisphere stroke; M ± SD: Age = 66 ± 13) took part in the study (the sample formed part of a larger cohort and was recruited in a context of a longitudinal study, see Fleury et al., 2022), 12 months after the stroke onset. Patients were enrolled in the current study if they had a stroke that led to unilateral upper limb motor impairment. We exclude patients with aphasia or neglect as it would have impacted their performance in this study, as well as patients with a cognitive score lower than 23 tested with the Montreal Cognitive Assessment test (MOCA; Nasreddine, 2005). Patients provided written informed consent following the local ethical committee (Vaud and Valais: 2016-02541) and the declaration of Helsinki (2013). The recruitment was blind to the level of motor impairment and lesion location (hemispheric location was known) to avoid any experimental bias during the study. That information was given to the experimenter after the study took place.

Neuropsychological and motor assessment

Neuropsychological assessment was performed by a trained neuropsychologist and is described in (Fleury et al., 2022). In this study, we made sure that the patient had no neglect or aphasia and a cognitive score equal to or above 23 (maximum score possible: 30) as tested with the MOCA (Nasreddine, 2005). The same neuropsychologist performed motor assessment. Both assessments were performed one week and twelve months after stroke onset. Hemispheric lesions' location and MOCA score are depicted in **Table 1**. **Supplementary Figure 1** depicts the motor abilities of the patients for both timepoints and **Supplementary Figure 2** depicts the lesions of each stroke patient.

Patient	Hemispheric location	MOCA score(Max score:30)	Gender
1	Right	28	F
2	Left	27	M
3	Right	29	M
4	Left	29	F
5	Left	28	M
6	Left	28	F
7	Left	25	M

Table 1. Hemispheric location and cognitive score of each patient. Hemispheric location, cognitive assessment measured using the Montreal cognitive assessment (MOCA) twelve months after stroke onset, and gender (F = female, M = male) of each patient.

Experimental design

Patients were sitting on a chair wearing a VR head-mounted display (HMD, Oculus Rifts S, refreshing rate 80Hz, resolution 1280 x 1440 per eye, 660 ppi). An infrared camera to track the upper limb movement of the patients and to project it in VR was hooked on the HMD. A foot pedal was placed on the floor just in front of the feet of the patient, with which patients could answer the questions asked during the task while ensuring that the upper limbs were free. The task consisted of four different sessions: (1) an incidental encoding session in VR, (2) autobiographical memory interview to measure autonoetic consciousness related to personal memories, (3) a recognition task in VR, (4) autonoetic consciousness related to the encoding in VR assessed one week after the encoding session.

Encoding

Patients were immersed in two virtual scenes containing 12 objects each and observed a virtual avatar from 1PP. They were instructed to move their unaffected upper limb (to ensure that each patient could manage to perform the movement no matter their level of motor impairment) between two black spheres appearing in the virtual scenes. To ensure that the location of the spheres did not affect the capacity of the patient to observe the whole scene, the black spheres were displayed on the left, then in front of the patients and finally on the right of the patients for 10s each time. The total duration of the scene observation was 30s. The spheres were displayed to trigger a horizontal movement. We ensured that the virtual upper limb did not hide the objects in the scene. Each scene was associated with a specific level of visuomotor congruency: in one condition, the virtual upper limb movements were synchronized with patients' upper limb movement (SYNCH1PP), therefore ensuring a visuomotor congruency. In a second condition, the virtual limb movements were delayed compared to patients' movement (with a delay ranging between 800 and 1000ms, ASYNCH1PP), thus inducing a mismatch in visuomotor integration. The association between scene and conditions was pseudorandomized between patients. The conditions were presented in alternance (e.g., SYNCH1PP followed by ASYNCH1PP) for 30 seconds each and repeated four times to facilitate encoding. An intertrial interval of five seconds was displayed between the presentation of each scene. Immediately after encoding the scenes, patients were immersed in a third, VR outdoor scene, in which they had to perform the same movement of encoding in both conditions (30s each, repeated twice). After each block of 30 seconds, a virtual knife appeared towards the virtual avatar to threaten the virtual body. We asked participants to answer five questions to assess their BSC. These included questions to assess SoA ("I felt that I was in control of the virtual avatar") , body ownership (" I felt that the virtual body was my body"), response to a threat (" I was afraid to be hurt by the knife"), and control for experimental bias ("I felt that the trees were my body", "I felt that I had more than three body"). The patients answered the questions by pressing the button on a foot pedal to move a slider on a continuous scale. The questions to assess BSC were asked in a different scene than the one encoded to ensure no interference with the encoding process for each scene.

Recognition task

One hour after the encoding, patients were immersed back in VR. After 10s of scene observation, patients had to tell whether the scene corresponded to the one seen at encoding or not (Patients had to answer to the question "Is there any change in the room compared to the first time you saw it?"). Lure trials (45 out of the total 100 trials) included the scene seen at encoding but with one object of changed shape or color. 10 attentional trials were added in the task with two or three objects changed or objects that changed location, to ensure that the patient observed the scene carefully and was not trying to simply detect object changes. Importantly, there was no avatar displayed in the recognition task and patients were not asked to move their upper limb, to keep the recognition task as neutral in term of SoA manipulation, and ensure that the difference shown were due to the experimental manipulation performed at encoding. There were 100 trials in total but the task was adapted to patients tiredness. Therefore two patients performed 50 trials only (25 trials with the scene encoded under visuomotor congruency, and 25 trials with the scene encoded under visuomotor mismatch).

Autonoetic consciousness for real life events

we also collected autobiographical memories for event that happened before the stroke onset (PRE) compared to events that happened after stroke onset (POST) to assess autonoetic consciousness for real life events. We asked patients about four autobiographical memories, two of which happened before the stroke (anything that happened two weeks before the stroke), and two which happened after the stroke (anything that happened two weeks after the stroke, but was not related to the stroke and did not happened in the last month). We asked them for one negative and one positive memory for each of these categories, in order to have a balanced effect of valence in between both time periods. The patients were recorded during the interview. They first had one minute to think about a specific event, after which the experimenter helped them by giving the word "family event" and "disease" to cue for positive and negative memory respectively. Once the patient had a memory in mind, they described it briefly, by trying to place the event in time and location as precisely as possible. We then asked them to give a title to the event, after which we asked them a series of questions (**Table 2**) derived from the memory characteristic questionnaire (MCQ, Johnson et al., 1988, and the Episodic autobiographical memory interview (Irish, 2008; Irish et al., 2011) to measure their related autonoetic consciousness for each of the memory.

autonoetic consciousness for virtual scenes

One week after the encoding of virtual scenes, we called the patients back to measure the autonoetic consciousness related to the two scenes encoded under visuomotor congruency (SYNCH1PP) and visuomotor mismatch (ASYNCH1PP) in VR. We used the same questionnaire (**Table 2**) as during the autobiographical memory interview. We asked them to focus on the encoding part and to briefly describe each scene to ensure that the questionnaire assessed episodic memory related to the right condition.

Data Analysis

For the BSC measures, we averaged the ratings given for each question category (SoA, sense of ownership, threat and control questions).

To quantify the performance, we removed the answer of the attentional trials. Although the statistical analysis was done on the binomial answer of each trial (1 = correct, 0 = uncorrect), for a better understanding of the figures, we computed the percentage of correct answers over all trials for each participant and each condition.

We divided the patient into two groups based on their sensitivity to the BSC manipulation: patients with a positive difference between SoA rated under visuomotor congruency compared to visuomotor mismatch were placed in the "Sensitive to BSC manipulation" group. Patients with no difference of SoA ratings between the visuomotor congruency and the visuomotor mismatch condition were placed in the "not sensitive to BSC manipulation" group.

To quantify the autonoetic consciousness of the patients related to the four events retrieved during the autobiographical memory interview, we first reversed the scale of the items 8, 9 and 11 from the autonoetic consciousness questionnaire (**Table 2**), to have consistantly higher ratings corresponds to a stronger recollection across the overall questionnaire items. We then computed an autonoetic consciousness score by summing the normalized score of each item of the questionnaire (detailed items are depicted in **Table 2**) for each patient and each memory.

We used the same approach to quantify the episodic memory for both scenes encoded in VR under the visuomotor congruency (SYNCH1PP) and visuomotor mismatch (ASYNCH1PP).

Statistical analysis

Behavioral analysis was applied using R (R Core Team, 2022) and R studio (RStudio, 2022). Linear mixed models were computed using the package *lme4* (Walker et al., 2015) and *lmerTest* (Christhenssen RHB et al., 2017). Figures were created using the package *ggplot2* (Wickam et al, 2016).

First, we quantified the sensitivity to our SoA manipulation during encoding using a linear mixed model with the BSC ratings (1 model for each of the 5 questions) as dependent variable, the condition as factor with two levels (SYNCH1PP vs. ASYNCH1PP) and the participant as random effect.

Then we quantified the effects of our manipulation on recognition performance. We compared the difference in recognition performance between the patients who were sensitive to our BSC manipulation and those who were not. We applied a mixed effect logistic regression model looking at recognition performance (binary, correct vs. incorrect) as a dependent variable with an interaction between conditions (factor, 2 levels, SYNCH1PP and

ASYNCH1PP) and the sensitivity to BSC (factor, two levels, sensitive to BSC manipulation and not sensitive to BSC manipulation) and the patients as random effect. In case of interaction, we applied a post-hoc mixed effect logistic regression to explain the recognition performance (binary, correct vs. incorrect) as a dependent variable with the conditions as fixed effect and participants as random effect for both groups (sensitive to BSC manipulation and not sensitive to BSC manipulation).

Next, we investigated the effect of valence and timing on the autonoetic consciousness of the personal memories of patients. We applied a linear mixed model to explain the autonoetic consciousness score as a dependent variable, with the timing (factor, two levels, PRE vs. POST stroke) as fixed effect and the patients as random effect. We applied a second linear mixed model to explain autonoetic consciousness score as dependent variable , the effect of valence (factor, two levels, positive vs. negative) as fixed effect and the patients as random effect.

Finally, we quantified the difference in autonoetic consciousness for the virtual scenes encoded under the different BSC manipulation (SYNCH1PP and ASYNCH1PP). We used a linear mixed model with the autonoetic consciousness score as dependent variable explained by the conditions (factor, two levels, SYNCH1PP, ASYNCH1PP) and the patients as random effect. To explore whether the sensitivity to our BSC manipulation impacted the difference, we also applied a linear mixed model to explain the autonoetic consciousness score by the interaction between conditions and sensitivity to the BSC manipulation (factor, two levels, sensitive to BSC manipulation and not sensitive to BSC manipulation).

Statement	Scale	Reference	# Index
My memory for this event involves sound	1-7 little/A lot	MCQ	1
My memory for this event involves smell	1-7 little/A lot	MCQ	2
My memory for this event involves touch	1-7 little/A lot	MCQ	3
The overall tone of the memory is	Negative/Neutral/Positive	MCQ	4
In this event I was	An observer /A participant	MCQ	5
I remember the event through my own eyes as during the event	1-7 Not at all/Definitely	MCQ	6
When you picture this event do you visualize it as a continuous video that plays with break, moving video clips with some breaks, one moving image or is it more like a set of snapshot with no movement, or something else?	1-7 One smooth video/video clips with breaks/one moving image/snapshot in sequence/one static snapshot/Hazy image/no image	EAMI	7
How often would you estimate you have thought about this memory since it first occurred?	1- 4 Frequently/Occasionnaly/Rarely/Never Never/Rarely/Occasionnaly/Frequently	EAMI	8
How often would you estimate you have spoken about this memory since it first occurred?	1-4 Frequently/Occasionnaly/Rarely/Never Never/Rarely/Occasionnaly/Frequently	EAMI	9
When you recall this event are you viewing the scene through your « own eyes » or can you see yourself in the memory from a third-person perspective?	Own eyes/Mixture/Third person/something different/no imagery	EAMI	10
When you recall this event how would you describe it in terms of vividness? This can apply to the richness of sights, sounds, smells, tastes, touch, and any movements you may have made.	1-7 very vivid/very vague 1-7 very vague/very vivid	EAMI	11

The relative spatial arrangement of people in my memory for the event is	1-7 Vague/Distinct	MCQ	12
My memory for the time when the event takes place is	1-7 Vague/Distinct	MCQ	13
When I remember the event, I see myself entirely in the scene as if I was watching a movie	1-7 Not at all/Definitely	MCQ	14
When I think about or tell this memory, I feel like I relive it as it happened	1-7 Not at all/Definitely	MCQ	15
I remember the movements and gestures I made with my body at the time of the event	1-7 / Vague/Distinct	In-house	16
My memory for this event is	1-7 Dim/Clear	MCQ	17
My memory for this event involves visual details	1-7 Little/ A lot	MCQ	18
My memory for this event is	1-7 Sketchy/very detailed	MCQ	19
My memory for the location where the event takes place is	1-7 Vague/Distinct	MCQ	20
Relative spatial arrangement of objects in my memory for the event is	1-7 Vague/Distinct	MCQ	21
When you think about this event now, do you re-experience any of the emotion you originally felt at the time? To what extent are you re-experiencing this emotion as a percentage?	0/25/50/75/100%	EAMI	22
To what extent are you re-experiencing this memory as a percentage?	0/25/50/75/100%	EAMI	23
Would you say you are reliving this memory or looking back on it?	Reliving/Looking back	EAMI	24
I remember how I felt at the time when the event took place	1-7 Not at all/Definitely	MCQ	25
I remember what I thought at the time	1-7 Not at all/Definitely	MCQ	26

Table 2. Questionnaire used to measure autonoetic consciousness for real life and virtual events. Questionnaire used to compute the autonoetic consciousness score related to the four real life event collected during the autobiographical memory interview . The same questionnaire was used to measure autonoetic consciousness related to the virtual scene encoded under different BSC states. Right column indicates whether the items were taken from the memory characteristic questionnaire (MCQ) or the episodic autobiographical memory interview (EAMI). Scale from original questionnaire is indicated in black, new scale is indicated in green.

5.4 Preliminary results

The results presented here are subject to change due to the small sample size (7 patients) acquired so far. We are planning to test ten more patients. The study was unfortunately slowed down heavily due to the pandemic situation.

We first tested the sensitivity of the patients to the visuomotor congruency manipulation induced during the encoding of virtual scenes. We found no significant effect of condition in the SoA ratings (estimate = -0.49, t = -2.1, p = 0.07, **Figure 1A),** ownership ratings (estimate = -0.46, t = -0.7, p = 0-5), nor in threat ratings (estimate = -0.38, t = -1.3, p = 0.23). There was also no difference in control ratings (estimate = -0.1, t = -1.48, p = 0.2). As depicted in **Figure 1A**, a detailed observation of the SoA ratings of each patient showed that four patients had increased SoA ratings in the condition with visuomotor congruency (SYNCH1PP) compared to the mismatch condition (ASYNCH1PP),therefore we labeled them "Sensitive to BSC manipulation". The remaining three patients had no difference in the SoA ratings between conditions and were labeled "Not sensitive to BSC manipulation".
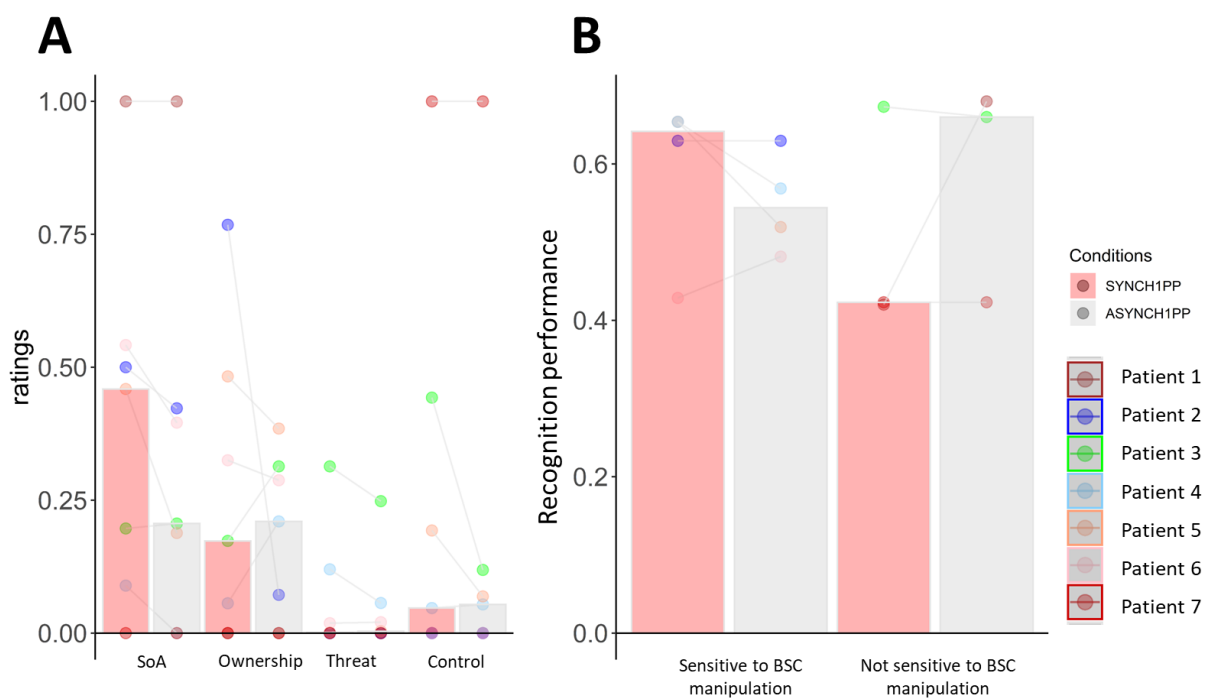
Figure 1. BSC measures and recognition performance. A. Ratings (continuous scale between 0 and 1) of sense of agency (SoA), Ownership, Threat and Control under visuomotor congruency (SYNCH1PP, red) and visuomotor mismatch (ASYNCH1PP, grey). B. Recognition performance (ratio of correct answers divided by number of trials) in patient sensitive to the BSC manipulation compared to patient not sensitive to the manipulation for scene encoded under visuomotor congruency (SYNCH1PP, red) and visuomotor mismatch (ASYNCH1PP, grey). Colored dots indicate individual data points.

Next, we investigated whether the difference of BSC sensitivity triggered difference of recognition performance. We found a marginal interaction between conditions and the group division of BSC sensitivity (estimate = 0.65, z = 1.9, p = 0.06). As observed in **Figure 1B**, this interaction was mainly triggered by two patients in the group sensitive to BSC manipulation

with higher recognition performance in the scene encoded under visuomotor congruency compared to visuomotor mismatch.

To better understand the effect of stroke on autobiographical memory, we compared the autonoetic consciousness score of patients on autobiographical memory encoded before and after the stroke onset (**Figure 2**). We found a significantly higher autonoetic consciousness score for memories that happened after stroke compared to before (estimate = 0.09, t = 2.94, p = 0.009). There was no effect of valence on patients' autonoetic consciousness (estimate = 0.06, t = 1.4, p = 0.18).
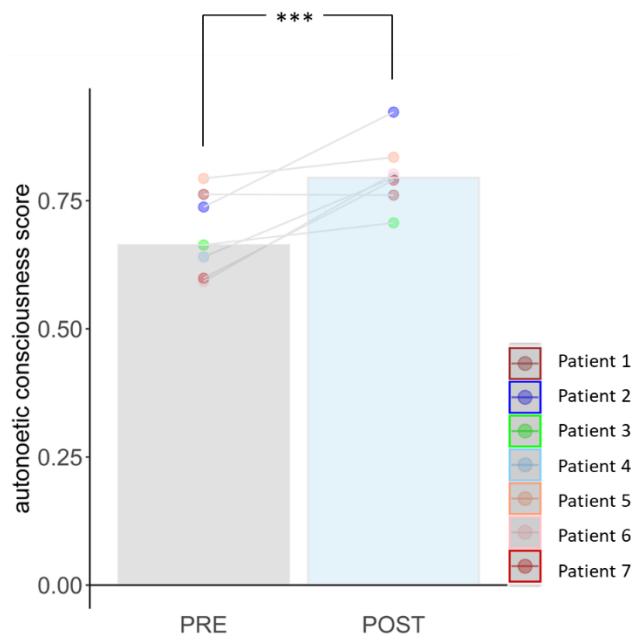
Figure 2. Autonoetic consciousness for real life events. autonoetic consciousness score of patient for events encoded before (PRE) and after (POST) stroke onset. *** indicate significance level with p-value <0.001 as tested with a linear mixed model with autonoetic consciousness score as dependent variable and conditions (PRE and POST) as fixed factor. Colored dots indicate individual data point. Autonoetic consciousness score was computed as the normalized sum of ratings of the autonoetic consciousness questionnaire for each condition.

Finally, we investigated the effect of BSC manipulation on autonoetic consciousness of the scene encoded in VR. We found not difference between conditions to explain the autonoetic consciousness score of patients (estimate = -0.01, t = -1.1, p = 0.3) and no significant interaction when taking into account the patients'sensitivity to the BSC manipulation (estimate = -0.001, -0.015, p = 0.98).

5.5 Discussion

In this proof-of-concept study, we tested the episodic memory of chronic stroke patients with lesions that led to upper limb motor impairment at stroke onset. We found that half of the patients were sensitive to our BSC manipulation. We observed that patients' sensitivity to BSC manipulation influenced the difference in recognition performance between conditions. Finally, we found that autonoetic consciousness for events that happened after stroke onset was significantly higher compared to events that happened before the stroke.

BSC deficit in stroke patients has been described in previous studies, most of them focusing on alterations of body ownership (Moro et al., 2016; Vallar & Ronchi, 2009). But although less reported, alterations of SoA in stroke patients was also outlined in the literature. Sensorimotor deficit of stroke is linked to SoA, with sensorimotor recovery leading to increased SoA for performed movement (Miyawaki et al., 2020a, 2020b). In this study we found no significant difference in SoA between conditions, suggesting that patients were not sensitive to our BSC manipulation at encoding. Interestingly, when looking at individual score, four patients seemed sensitive to the BSC manipulation, with higher ratings of SoA under visuomotor congruency compared to visuomotor mismatch, similar to what is detailed in study on young healthy participants (Kilteni et al., 2012; Padilla-Castañeda et al., 2014). The three remaining patients had no difference of SoA ratings between conditions. Although SoA in stroke patients has not been widely investigated, some studies investigated SoA deficit in schizophrenia patients (Garbarini et al., 2016; Hauser et al., 2011; Maeda et al., 2013; Synofzik & Voss, 2010). They proposed that SoA deficit in schizophrenia patients could be due to sensorimotor alteration (Jeannerod, 2009; Maeda et al., 2012, 2013). Here we propose that the difference of sensitivity between patients found in our study could be due to difference in the success of sensorimotor integration caused by the stroke lesions.

Although several studies demonstrated that patients with severe cortical lesions were more likely to have memory impairment (Nys et al., 2005; Schouten et al., 2009), only a few studies investigated the impact of sensorimotor alterations on memory. To our knowledge, two studies on rats showed that sensorimotor stroke altered the hippocampal-thalamic connectivity and led to impaired motor coordination and spatial memory deficit (Bouet et al., 2010; McCormick et al., 2015). In this study, we report a slight difference of recognition performance based on patients' sensitivity to BSC manipulation. Although the sample size is too small to draw any robust conclusion, future studies should investigate the association between patients' BSC sensitivity and recognition performance to better understand if sensorimotor deficit leads to reduced episodic memory impairment.

Only a few studies investigated autobiographical memory in stroke patients and the results described are very variable. While some studies did not find any difference between stroke patients and control patients for autobiographical memory (Sampson et al., 2003), other studies highlighted hemispheric specificities for altered autobiographical memory

(Hochstenbach et al., 1998; Schouten et al., 2009). Our study observed higher autonoetic consciousness for autobiographical events encoded after compared to before stroke onset. While a control group is necessary to ensure that the findings are not confounded with the recency of the memory (Piolino et al., 2006; Rubin & Wenzel, 1996), we argue that a recency effect is less likely to cause such difference, as we made sure the memory retrieved after stroke were at least one month old. Moreover, as patients could choose any events before stroke onset, we would have expected higher autonoetic consciousness for memories before stroke onset, as they are more likely to be personally relevant for the patients.

As the brain endures plasticity changes to cope with the lesioned areas after a stroke (Hallett, 2001; Rossini et al., 2007), we propose that the higher autonoetic consciousness for events happening after stroke onset is due to higher similarity in the brain activity during encoding and retrieval. This would suggest that autonoetic consciousness for events encoded before stroke onset is reduced to the stroke lesions and the altered sensorimotor integration.

To conclude, in this study, we observed differences in sensitivity to BSC manipulation and difference in memory performance depending on the patients' sensitivity to BSC manipulation. Finally, we reported higher autonoetic consciousness for events encoded after stroke, and we proposed that this difference is mainly due to plasticity changes after the lesions. This study is not without limitations. The small sample size, the variability of the level of impairment, and the unbalanced hemispheric lesions location do not allow for strong claims. However, this proof-of-concept study showed that it is of interest to test episodic memory and autonoetic consciousness in stroke patients. The variability in sensitivity to BSC manipulation could help understand the neural correlates of BSC and its links with sensorimotor alterations. Moreover, this population could further improve our understanding of the association between sensorimotor aspects of BSC and episodic memory.

5.6 References

Baumgartner, P., El Amki, M., Bracko, O., Luft, A. R., & Wegener, S. (2018). Sensorimotor stroke alters hippocampo-thalamic network activity. *Scientific Reports*, *8*(1), Art. 1. https://doi.org/10.1038/s41598-018-34002-9

Bergouignan. (2021). *Full article : Out-of-body memory encoding causes third-person perspective at recall*. https://www.tandfonline.com/doi/full/10.1080/20445911.2021.1958823

Bergouignan, L., Nyberg, L., & Ehrsson, H. H. (2014). Out-of-body–induced hippocampal amnesia. *Proceedings of the National Academy of Sciences*, *111*(12), 4421-4426. https://doi.org/10.1073/pnas.1318801111

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature Reviews Neuroscience*, *13*(8), Art. 8. https://doi.org/10.1038/nrn3292

Blanke, O., Slater, M., & Serino, A. (2015). Behavioral, Neural, and Computational Principles of Bodily Self-Consciousness. *Neuron*, *88*(1), 145-166. https://doi.org/10.1016/j.neuron.2015.09.029

Boccia, M., Teghil, A., & Guariglia, C. (2019). Looking into recent and remote past : Meta-analytic evidence for cortical re-organization of episodic autobiographical memories. *Neuroscience & Biobehavioral Reviews*, *107*, 84-95. https://doi.org/10.1016/j.neubiorev.2019.09.003

Bosch, S. E., Jehee, J. F. M., Fernández, G., & Doeller, C. F. (2014). Reinstatement of Associative Memories in Early Visual Cortex Is Signaled by the Hippocampus. *Journal of Neuroscience*, *34*(22). https://doi.org/10.1523/JNEUROSCI.0805-14.2014

Bouet, V., Freret, T., Ankri, S., Bezault, M., Renolleau, S., Boulouard, M., Jacotot, E., Chauvier, D., & Schumann-Bard, P. (2010). Predicting sensorimotor and memory deficits after neonatal ischemic stroke with reperfusion in the rat. *Behavioural Brain Research*, *212*(1), 56-63. https://doi.org/10.1016/j.bbr.2010.03.043

Bréchet, L., Mange, R., Herbelin, B., Theillaud, Q., Gauthier, B., Serino, A., & Blanke, O. (2019). First-person view of one's body in immersive virtual reality : Influence on episodic memory. *PLOS ONE*, *14*(3), e0197763. https://doi.org/10.1371/journal.pone.0197763

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

Corcoran, R., & Frith, C. D. (2003). Autobiographical memory and theory of mind : Evidence of a relationship in schizophrenia. *Psychological Medicine*, *33*(5), 897-905. https://doi.org/10.1017/S0033291703007529

Fleury, L., Koch, P. J., Wessel, M. J., Bonvin, C., Millan, D. S., Constantin, C., Vuadens, P., Adolphsen, J., Cadic-Melchior, A. G., Brügger, J., Beanato, E., Ceroni, M., Menoud, P., Rodriguez, D. de L., Zufferey, V., Meyer, N., Egger, P., Harquel, S., Popa, T., … Hummel, F. C. (2022). *Towards individualized Medicine in Stroke – the TiMeS project : Protocol of longitudinal, multi-modal, multi-domain study in stroke* (p. 2022.05.18.22274612). medRxiv. https://doi.org/10.1101/2022.05.18.22274612

Garbarini, F., Mastropasqua, A., Sigaudo, M., Rabuffetti, M., Piedimonte, A., Pia, L., & Rocca, P. (2016). Abnormal Sense of Agency in Patients with Schizophrenia : Evidence from Bimanual Coupling Paradigm. *Frontiers in Behavioral Neuroscience*, *10*. https://www.frontiersin.org/articles/10.3389/fnbeh.2016.00043

Gauthier, B., Bréchet, L., Lance, F., Mange, R., Herbelin, B., Faivre, N., Bolton, T. A. W., Ville, D. V. D., & Blanke, O. (2020). First-person body view modulates the neural substrates of episodic memory and autonoetic consciousness : A functional connectivity study. *NeuroImage*, *223*, 117370. https://doi.org/10.1016/j.neuroimage.2020.117370

Hallett, M. (2001). Plasticity of the human motor cortex and recovery from stroke. *Brain Research Reviews*, *36*(2), 169-174. https://doi.org/10.1016/S0165-0173(01)00092-3

Hauser, M., Knoblich, G., Repp, B. H., Lautenschlager, M., Gallinat, J., Heinz, A., & Voss, M. (2011). Altered sense of agency in schizophrenia and the putative psychotic prodrome. *Psychiatry Research*, *186*(2), 170-176. https://doi.org/10.1016/j.psychres.2010.08.003

Hochstenbach, J., van Spaendonck, K. P., Cools, A. R., Horstink, M. W., & Mulder, T. (1998). Cognitive deficits following stroke in the basal ganglia. *Clinical Rehabilitation*, *12*(6), 514-520. https://doi.org/10.1191/026921598666870672

Irish. (2008). *Assessment of behavioural markers of autonoetic consciousness during episodic autobiographical memory retrieval : A preliminary analysis—IOS Press*. https://content.iospress.com/articles/behavioural-neurology/ben00190

Irish. (2011). *Elsevier Enhanced Reader*. https://reader.elsevier.com/reader/sd/pii/S0028393211002661?token=890DE9E7DA8CDEC9F30F0D25238FDC9E64A0DFEB84F3 8ECCC7A4BCD88645A1D3B4FBBC18DA7F42C86EC9C0023590A66A&originRegion=eu-west-1&originCreation=20221004220842

Iriye, H., & Ehrsson, H. H. (2022). Perceptual illusion of body-ownership within an immersive realistic environment enhances memory accuracy and re-experiencing. *IScience*, *25*(1), 103584. https://doi.org/10.1016/j.isci.2021.103584

Iriye, H., & St. Jacques, P. L. (2021). Memories for third-person experiences in immersive virtual reality. *Scientific Reports*, *11*(1), Art. 1. https://doi.org/10.1038/s41598-021-84047-6

Jeannerod, M. (2009). The sense of agency and its disturbances in schizophrenia : A reappraisal. *Experimental Brain Research*, *192*(3), 527-532. https://doi.org/10.1007/s00221-008-1533-3

Johnson, M. K., Foley, M. A., Suengas, A. G., & Raye, C. L. (1988). Phenomenal characteristics of memories for perceived and imagined autobiographical events. *Journal of Experimental Psychology: General*, *117*, 371-376. https://doi.org/10.1037/0096-3445.117.4.371

Kilteni, K., Groten, R., & Slater, M. (2012). The Sense of Embodiment in Virtual Reality. *Presence: Teleoperators and Virtual Environments*, *21*(4), 373-387. https://doi.org/10.1162/PRES_a_00124

Lim, C., & Alexander, M. P. (2009). Stroke and episodic memory disorders. *Neuropsychologia*, *47*(14), 3045-3058. https://doi.org/10.1016/j.neuropsychologia.2009.08.002

Maeda, T., Kato, M., Muramatsu, T., Iwashita, S., Mimura, M., & Kashima, H. (2012). Aberrant sense of agency in patients with schizophrenia : Forward and backward over-attribution of temporal causality during intentional action. *Psychiatry Research*, *198*(1), 1-6. https://doi.org/10.1016/j.psychres.2011.10.021

Maeda, T., Takahata, K., Muramatsu, T., Okimura, T., Koreki, A., Iwashita, S., Mimura, M., & Kato, M. (2013). Reduced sense of agency in chronic schizophrenia with predominant negative symptoms. *Psychiatry Research*, *209*(3), 386-392. https://doi.org/10.1016/j.psychres.2013.04.017

Markowitsch, H. J., & Staniloiu, A. (2011). Memory, autonoetic consciousness, and the self. *Consciousness and Cognition*, *20*(1), 16-39. https://doi.org/10.1016/j.concog.2010.09.005

McCormick, C., St-Laurent, M., Ty, A., Valiante, T. A., & McAndrews, M. P. (2015). Functional and Effective Hippocampal–Neocortical Connectivity During Construction and Elaboration of Autobiographical Memory Retrieval. *Cerebral Cortex*, *25*(5), 1297-1305. https://doi.org/10.1093/cercor/bht324

Meer, M. P. A. van, Marel, K. van der, Wang, K., Otte, W. M., Bouazati, S. el, Roeling, T. A. P., Viergever, M. A., Sprenkel, J. W. B. van der, & Dijkhuizen, R. M. (2010). Recovery of Sensorimotor Function after Experimental Stroke Correlates with Restoration of Resting-State Interhemispheric Functional Connectivity. *Journal of Neuroscience*, *30*(11), 3964-3972. https://doi.org/10.1523/JNEUROSCI.5709-09.2010

Miyawaki, Y., Otani, T., & Morioka, S. (2020a). Agency judgments in post-stroke patients with sensorimotor deficits. *PLOS ONE*, *15*(3), e0230603. https://doi.org/10.1371/journal.pone.0230603

Miyawaki, Y., Otani, T., & Morioka, S. (2020b). Dynamic Relationship between Sense of Agency and Post-Stroke Sensorimotor Deficits : A Longitudinal Case Study. *Brain Sciences*, *10*(5), Art. 5. https://doi.org/10.3390/brainsci10050294

Moro, V., Pernigo, S., Tsakiris, M., Avesani, R., Edelstyn, N. M. J., Jenkinson, P. M., & Fotopoulou, A. (2016). Motor versus body awareness : Voxel-based lesion analysis in anosognosia for hemiplegia and somatoparaphrenia following right hemisphere stroke. *Cortex*, *83*, 62-77. https://doi.org/10.1016/j.cortex.2016.07.001

Moscovitch, M., Rosenbaum, R. S., Gilboa, A., Addis, D. R., Westmacott, R., Grady, C., McAndrews, M. P., Levine, B., Black, S., Winocur, G., & Nadel, L. (2005). Functional neuroanatomy of remote episodic, semantic and spatial memory : A unified account based on multiple trace theory. *Journal of Anatomy*, *207*(1), 35-66. https://doi.org/10.1111/j.1469-7580.2005.00421.x

Nadel, L., Samsonovich, A., Ryan, L., & Moscovitch, M. (2000). Multiple trace theory of human memory : Computational, neuroimaging, and neuropsychological results. *Hippocampus*, *10*(4), 352-368. https://doi.org/10.1002/1098-1063(2000)10:4<352::AID-HIPO2>3.0.CO;2-D

Nasreddine. (2005). *The Montreal Cognitive Assessment, MoCA: A Brief Screening Tool For Mild Cognitive Impairment*. https://agsjournals.onlinelibrary.wiley.com/doi/full/10.1111/j.1532-5415.2005.53221.x

Nys, G. M. S., Zandvoort, M. J. E. V., Kort, P. L. M. D., Jansen, B. P. W., Worp, H. B. V. D., Kappelle, L. J., & Haan, E. H. F. D. (2005). Domain-specific cognitive recovery after first-ever stroke : A follow-up study of 111 cases. *Journal of the International Neuropsychological Society*, *11*(7), 795-806. https://doi.org/10.1017/S1355617705050952

Padilla-Castañeda, M. A., Frisoli, A., Pabon, S., & Bergamasco, M. (2014). The Modulation of Ownership and Agency in the Virtual Hand Illusion under Visuotactile and Visuomotor Sensory Feedback. *Presence*, *23*(2), 209-225. https://doi.org/10.1162/PRES_a_00181

Park, H.-D., & Blanke, O. (2019). Coupling Inner and Outer Body for Self-Consciousness. *Trends in Cognitive Sciences*, *23*(5), 377-388. https://doi.org/10.1016/j.tics.2019.02.002

Piolino, P., Desgranges, B., Clarys, D., Guillery-Girard, B., Taconnat, L., Isingrini, M., & Eustache, F. (2006). Autobiographical memory, autonoetic consciousness, and self-perspective in aging. *Psychology and Aging*, *21*(3), 510-525. https://doi.org/10.1037/0882-7974.21.3.510

Prebble, S. C., Addis, D. R., & Tippett, L. J. (2013). Autobiographical memory and sense of self. *Psychological Bulletin*, *139*, 815-840. https://doi.org/10.1037/a0030146

Ricarte, J. J., Ros, L., Latorre, J. M., & Watkins, E. (2017). Mapping autobiographical memory in schizophrenia : Clinical implications. *Clinical Psychology Review*, *51*, 96-108. https://doi.org/10.1016/j.cpr.2016.11.004

Rossini, P. M., Altamura, C., Ferreri, F., Pasqualetti, P., & Vernieri, F. (2007). Neuroimaging experimental studies on brain plasticity in recovery from stroke. *EUROPA MEDICOPHYSICA*, *43*(2), 15.

Rubin, D. C., & Wenzel, A. E. (1996). One hundred years of forgetting : A quantitative description of retention. *Psychological Review*, *103*, 734-760. https://doi.org/10.1037/0033-295X.103.4.734

Ryan, L., Nadel, L., Keil, K., Putnam, K., Schnyer, D., Trouard, T., & Moscovitch, M. (2001). Hippocampal complex and retrieval of recent and very remote autobiographical memories : Evidence from functional magnetic resonance imaging in neurologically intact people. *Hippocampus*, *11*(6), 707-714. https://doi.org/10.1002/hipo.1086

Sampson, M. J., Kinderman, P., Watts, S., & Sembi, S. (2003). Psychopathology and autobiographical memory in stroke and non-stroke hospitalized patients. *International Journal of Geriatric Psychiatry*, *18*(1), 23-32. https://doi.org/10.1002/gps.763

Schouten, E. A., Schiemanck, S. K., Brand, N., & Post, M. W. M. (2009). Long-Term Deficits in Episodic Memory after Ischemic Stroke : Evaluation and Prediction of Verbal and Visual Memory Performance Based on Lesion Characteristics. *Journal of Stroke and Cerebrovascular Diseases*, *18*(2), 128-138. https://doi.org/10.1016/j.jstrokecerebrovasdis.2008.09.017

Synofzik, M., & Voss, M. (2010). Disturbances of the Sense of Agency in Schizophrenia. In B. Michela (Éd.), *Neuropsychology of the Sense of Agency : From Consciousness to Action* (p. 145-155). Springer Milan. https://doi.org/10.1007/978-88-470-1587-6_8

Tsakiris, M., Hesse, M. D., Boy, C., Haggard, P., & Fink, G. R. (2007). Neural Signatures of Body Ownership : A Sensory Network for Bodily Self-Consciousness. *Cerebral Cortex*, *17*(10), 2235-2244. https://doi.org/10.1093/cercor/bhl131

Tsakiris, M., Longo, M. R., & Haggard, P. (2010). Having a body versus moving your body : Neural signatures of agency and body-ownership. *Neuropsychologia*, *48*(9), 2740-2749. https://doi.org/10.1016/j.neuropsychologia.2010.05.021

Tulving. (1985). *tulving semantic and episodic memory—Google Scholar*. https://scholar.google.com/scholar?hl=fr&as_sdt=0%2C49&q=tulving+semantic+and+episodic+memory&btnG=

Vallar, G., & Ronchi, R. (2009). Somatoparaphrenia : A body delusion. A review of the neuropsychological literature. *Experimental Brain Research*, *192*(3), 533-551. https://doi.org/10.1007/s00221-008-1562-y

WANG, Q., & CONWAY, M. A. (2006). Autobiographical Memory, Self, and Culture. In *Memory and Society*. Psychology Press.

Wheeler. (2000). *Memory's echo : Vivid remembering reactivates sensory-specific cortex | PNAS*. https://www.pnas.org/doi/abs/10.1073/pnas.97.20.11125

5.7 Supplementary Information
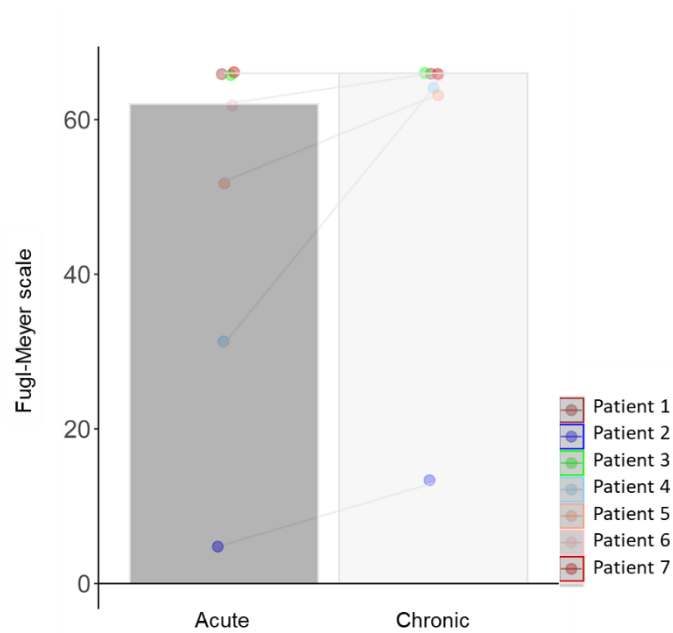
Supplementary Figure 1. Motor abilities assessed with the Fugl-Meyer scale in the acute and chronic stage of the stroke.
Fugl-meyer score (maximum = 66) assessed one week after stroke (acute stage , dark grey) and twelve months after stroke (chronic stage , light grey). Colored dots depict individual data points.
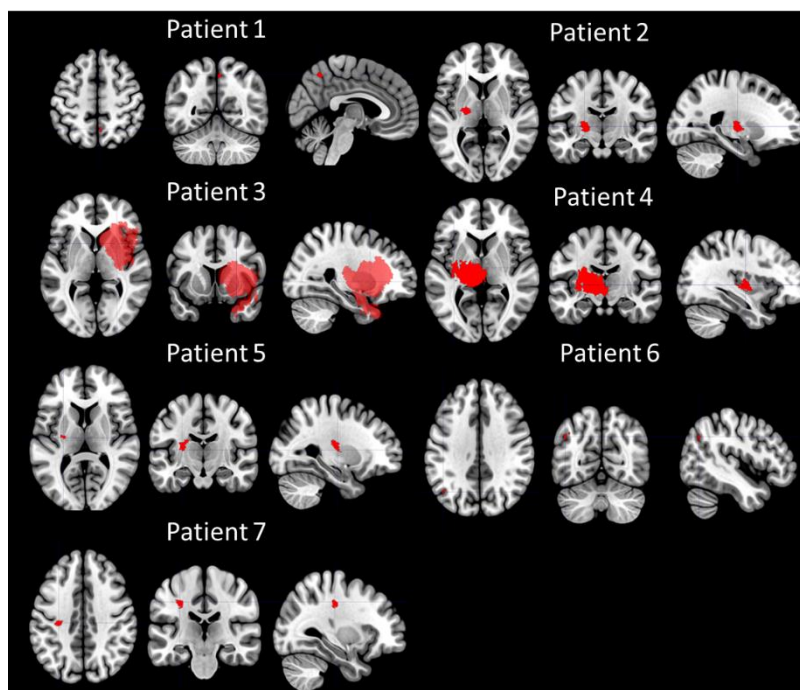
Supplementary Figure 2. *Lesions of the patients one week after stroke onset.*

6. Study 5: Bodily illusions in virtual reality: new insights into how VR influence embodiment

Authors

Nathalie Heidi Meyer[1]*, Sophie Betka[1]*, Baptiste Gauthier[2], Elizabeth Franc[1], Juliette Boscheron[1], Bruno Herbelin[1], Florian Lance[1], Olaf Blanke[1,3]

Affiliations

[1] Laboratory of Cognitive Neuroscience, Neuro-X Institute & Brain Mind Institute and Center for Neuroprosthetics, Faculty of Life Sciences, Ecole Polytechnique Fédérale de Lausanne, Geneva, Switzerland

[2] Clinical Research Unit, Neuchâtel Hospital Network, 2000 Neuchâtel, Switzerland

[3] Department of Clinical Neurosciences, University Hospital Geneva, Rue Micheli-du-Crest 24, 1205, Geneva Switzerland

*Equal contributions

6.1 Abstract

Virtual reality (VR) allows the study of ecological human behaviors within controlled environments. Precise optimization of VR characteristics is required to induce a subjective experience in VR, similar to the one experienced in real life. On the one hand, VR researchers quantify participants' sense of ownership (SoO) and sense of agency (SoA) towards a virtual avatar to measure the realism of VR experience. On the other hand, scientists studying bodily self-consciousness (BSC, i.e., lower-level self-consciousness informed by the multisensory integration of bodily signals) benefit from the improvement of VR to induce bodily illusions. SoA and SoO are also used to measure the strength of such induced illusions. Therefore, investigating the VR features necessary to generate robust SoA and SoO is interesting for both VR and BSC research fields. In this study, we measured the VR experience of participants during four VR-based BSC experiments. We found that SoO depends on the physical characteristics of the avatar such as its size. Immersion was positively related to SoO and significantly decreased in VR-MRI settings compared to classical settings (i.e. outside the scanner, using a Head-mounted display). Finally, we also described participants' spontaneous feedback regarding the quality of their VR experience. Our results encourage future studies to improve VR experience by enhancing avatar resemblance with participants through adjustment of skin tone and size. Such findings should also be applied to VR-MRI settings to boost immersion.

6.2 Introduction

Virtual reality (VR) is a powerful technology that has been widely used in the last decades within the field of cognitive neuroscience (Pan & Hamilton, 2018; Skurla et al., 2022). The main advantage of VR is to create immersive virtual environments while maintaining high control over complex virtual scenarios, thus increasing the reproducibility of studies (Pan & Hamilton, 2018). VR also allows to study situations that could not be tested in real life due to their dangerous aspects, such as the behavioral response to violent incidents (Slater et al., 2013, 2022). Additionally, the use of avatars in VR allows to induce experience that could not be possible in real life, such as experiencing the world as a child or with a perspective change in a virtual scenario (Debarba et al., 2017; Gonzalez-Franco & Lanier, 2017; Tajadura-Jiménez et al., 2018).

One of the cognitive fields that benefits from such technology is the field of bodily self-consciousness (BSC), which study the emergence of the experience of the unitary self arising from the multisensory and sensorimotor integration of bodily signals (Blanke, 2012; Blanke et al., 2015). It is proposed that the integration of multiple sensory signals creates the sense of ownership (SoO), the feeling that the body belongs to oneself, and sense of agency (SoA), the feeling of being in control of the action performed with one's body (Blanke, 2012; Blanke et al., 2015; Haggard, 2017; Pyasik et al., 2018). A significant breakthrough in the field of BSC sits in the creation of the rubber hand illusion paradigm. Such paradigm generates an illusory experience of SoO towards a rubber hand. In this experiment, a researcher is stroking the back of a participant's hand hidden outside their field of view while synchronously stroking a rubber hand placed in front of the participant. The synchronous integration of the tactile signals felt by the stroking with the vision of the simultaneous stroking on the rubber hand creates the illusory of SoO towards the rubber hand (Botvinick & Cohen, 1998). VR allows the production of illusions using different sensory modalities. For example, visuomotor congruency between users' movement and an observed avatar in VR, generates an illusory feeling of SoA towards the avatar (Imaizumi & Asai, 2015; Kilteni et al., 2012; Weijs et al., 2021). Conversely, the induction of a delay between the users' movement and the observed avatar movement alters BSC and its related SoA (Kilteni et al., 2012). Therefore, using VR, experimenters can modulate BSC and measure the subjective experience related to altered BSC components, such as SoO or SoA.

The study of human cognition in VR revolves around the critical ability of VR environment to trigger ecologically valid behavior that could be observed in real-life (Sanchez-Vives & Slate, 2005). Therefore, it is interesting to understand the parameters in VR necessary to produce such real-life behavior. Moreover, a tight balance needs to be achieved in VR to have features that are realistic enough to trigger lifelike behavior while avoiding falling into the "uncanny valley", where VR features are realistic but not convincing enough to immerse the participants in the VR environment (Mori et al., 2012). A central aspect to trigger naturalistic behavior is

the crucial need for immersion (also called sense of presence), defined as the subjective feeling of presence in the virtual environment (North & North, 2016; Servotte et al., 2020).

In the last decades, studies have investigated the relationship between VR features and immersion, showing that increased screen resolution, field of view and realism of avatar characteristics improved immersion (Bowman & McMahan, 2007; Ogawa et al., 2018). In that light, SoO and SoA have been investigated in both VR and BSC fields. The VR field uses the combination of SoO and SoA referred to as "embodiment" (Fribourg et al., 2020; Kilteni et al., 2012) to measure the quality of VR experience related to some specific VR features such as realism, immersion and avatar appearance (Freude et al., 2020; Mühlberger et al., 2015, Jo et al., 2017; Waltemate et al., 2018). For example, skin tone and avatar gender are important avatar characteristics that can boost the embodiment when adequately matched with the participants' appearance (Lira et al., 2017; Schwind et al., 2017). In the BSC field, researchers rely on a good embodiment of virtual avatar and use SoO and SoA to measure the strength of the bodily illusion induced using sensory congruency (Kilteni et al., 2012, 2015; Pozeg et al., 2015; Yuan & Steed, 2010). Therefore, understanding how SoO and SoA are affected by VR features would benefit both researchers in the VR field to optimize VR experience and researchers in the BSC field to enhance bodily illusion towards an avatar in VR environments.

Although several studies described how VR features impact BSC measurements, the constant improvement of VR technology highlights the crucial need to continue studying the relationship between VR features and BSC. This study investigated the association between VR features, SoA and SoO. Specifically, we investigated the user experience related to avatar resemblance, immersion, avatar movement, avatar realism and avatar size, as well as the relationship between such features and BSC measurements (SoA and SoO). We then investigated the effect of gender on VR features and BSC measurements. Of particular interest, we bring novel insight into the level of immersion in VR performed in an MR-scanner. Finally, in light of the existing literature, we discussed the necessary improvements to boost immersion and increase the quality of future BSC research using VR.

6.3 Methods

Participants

We recruited 109 right-handed participants (Experiment 1: N = 26, 7 males, mean age 23 ± 3.4 years, Experiment 2: N = 29, 11 males, 3 gender-nonconforming, mean age 24 ± 3.4 years, Experiment 3: N = 27, 10 males, mean age 27 ± 3.5, Experiment 4, N = 27, 11 males; mean age 25 ± 3.4 years). Participants reported no history of neurological and psychiatric disorders and no drug consumption in the 48 hours before the experiment. Participants provided written informed consent following the local ethical committee guidelines (Cantonal Ethical Committee of Geneva: 2015-00092, and Vaud and Valais: 2016-02541) and the declaration of Helsinki (2013). Participants were financially compensated for their participation.

Study design

We collected feedback reports from participants involved in four experiments combining VR and motion tracking (for a detailed description see Meyer & Gauthier, in prep). During each experiment, participants were lying in a replicate of an MR-scanner (Experiment 1, 3,4) or an MR-scanner (Experiment 2) and were immersed in VR (Experiment 1,3,4: Oculus Rifts S, refreshing rate 80Hz, resolution 1280 x 1440 per eye, 660 ppi; Experiment 2: MRI-compatible goggle, Visual System HD, NordicNeuroLab, Bergen, Norway). They were instructed to move their right limb while observing an avatar in different virtual environments **(Figure 1).** The avatar was matched with the gender of the participants and the avatar skin tone (three tones possible) was adjusted to be as close as possible to the participant's skin tone. In Each experiment, participants observed the avatar in three different conditions: (1) the avatar was observed in the most ecological condition, at the first-person perspective with synchronization between the participant's and the avatar's movements (synchronous 1PP condition); (2) the avatar was observed from the first-person perspective with a fluctuating delay (800-1000ms) induced between the participant's and avatar's movements (asynchronous 1PP condition); (3) the avatar was observed from the third -person perspective with a fluctuating delay (800-1000ms) induced between the participant's and avatar's movements (asynchronous 3PP condition); see Meyer & Gauthier, in prep for further details*).*

Figure 1. Setup description. *Participants were laying down a mock MR-scanner (Experiment 1,3 and 4) or a MR-scanner (Experiment 2). They were immersed into the virtual scenes with an Head Mounted Display (HMD; Experiment 1, 3 and 4) or MRI-compatible virtual reality goggle (1). They were holding tennis ball on which reflective marker were placed (2) to track the movement of the upper limb using infrared camera attached to the ceiling (3). Lower panel: View of a scene with a male avatar (left) and a female avatar (right).*

In the current paper, we were interested only in the most ecological condition (i.e., synchronous 1PP condition) provided by a naturalistic first-person perspective and synchronized movement between participants and the avatar in VR. After being exposed to the first-person perspective synchronized condition in each experiment, a virtual knife appeared and moved in the avatar's direction. After this, we measured participants' BSC using five questions presented successively and in a randomized order (**Table 1**) to quantify their level of SoA, SoO, and control for experimental bias. We distinguished two ratings for SoO. One question was explicitely measuring the SoO of participants towards the avatar (Q2:" I felt that the virtual body was mine"), therefore considered as explicit (SoO$_{explicit}$). We asked a second question to measure SoO implicitely (SoO$_{implicit}$; Q3 "I was afraid to be hurt by the knife").

Questions		BSC measurements
Q1	I felt that I was controlling the virtual body	Sense of agency (SoA)
Q2	I felt that the virtual body was mine	Explicit sense of ownership (SoO$_{explicit}$)
Q3	I was afraid to be hurt by the knife	Implicit sense of ownership (SoO$_{implicit}$)
Q4	I felt like I had more than three bodies	Control for experimental bias
Q5	I felt like the trees were my body	Control for experimental bias

Table 1. BSC measurements question. *Questions used to measure sense of agency (SoA), explicit sense of ownership (SoO$_{explicit}$), implicit sense of ownership (SoO$_{implicit}$) and control for experimental bias using a continuous scale.*

At the end of each experiment, participants were first asked to freely report their experience in VR and then to evaluate VR features by rating 5 items (see **Table 2**) using a 7-points scale (1 = strongly disagree, 7 = strongly agree).

	Questions	VR features
Q1	the appearance of the avatar looked like me	Resemblance
Q2	How much did you feel immersed in the virtual environments	Immersion
Q3	The movement of the avatar were realistic	Movement
Q3a	When there was no bug, the movement of the avatar was realistic	Movement
Q3b	When there was some bug, the movement of the avatar was realistic	Movement
Q4	the avatar was realistic	Realism
Q5	The avatar size was my size	Size

Table 2. questions on VR features. *Items used to measure VR features (avatar resemblance, immersion, avatar movement, avatar realism, and avatar size) at the end of the experiment with a 7-points scale.*

After collecting the data in Experiment 1, we added the question about immersion (Q2) and we refined the question about movement (Q3). We realized that the question regarding the avatar movement was not straightforward because the avatar movements were synchronized with the participant movement in one condition but also observed with a delay compared to the participants' movements in two others. Therefore, in the following experiments (Experiment 2, 3, and 4), when the participant spontaneously reported a delay of synchronization (often reported as a "bug"), Q3 was separated into two new questions (Q3a: "When there was no bug, the movement of the avatar was realistic" and Q3b: "When there was some bug, the movement of the avatar was realistic", see **Table 1**).

Data Analysis

Data from 3 participants (2 in Experiment 1, 1 in Experiment 3) and 5 participants (2 in Experiment 1, 2 in Experiment 2, and 1 in Experiment 4) were discarded due to technical issues during the task or because they did not understand the BSC questions during the BSC assessment. Also, resemblance ratings are missing for one participant in Experiment 1. We merged data from the four experiment (Experiment 1, 2, 3 and 4). Analyses were thus performed on a total of 101 participants (100 for the analysis focusing on resemblance).To facilitate the interpretation of our results, we averaged the ratings of the two control questions of the BSC assessment (see **Table 1**, Q4 and Q5) to obtain one score representing the overall experimental bias. We performed all the statistical analysis on normalized VR feature ratings from the 7-points scale and transformed the ratings in percentages for the figures.

Statistical Analysis

All analyses were performed in the R environment (R Core Team, 2022, version 4.2.1) using Rstudio (RStudio, 2022, version 4.2.1)
For each analysis of variance (ANOVA) performed, in case of significant main effect and/or interaction, *post-hoc* pairwise comparisons were computed and Bonferroni corrections were applied, using the *multcomp* package (Torsten Hothorn, Frank Bretz and Peter Westfall , 2008).

First, we computed the means and standard deviations of the VR features (i.e. Resemblance, Immersion, Movement, Realism, and Size, see **Table 2**) to describe our sample. Then, we tested for a main effect of VR features, using a one-way repeated measures ANOVA. All results were corrected for multiple comparisons using the Bonferonni corrections. Detailed tables for each experiment are given in the supplementary section (See **Table S1- S4**) and were created using the R package *vtable* (Huntington-Klein N , 2022).

Secondly, we explored the relationships between the VR features and the BSC measurements. To do so, we applied a one-way ANOVA on the BSC measurements to verify that they were higher than the questions to control for experimental bias (adjusted p-values using Bonferroni correction = 0.05/ 6= 0.008). We then computed Pearson correlations for each relationship between the five VR features (Resemblance, Immersion, Movement, Realism, and Size) and the 3 BSC measurements (SoO$_{implicit}$, SoO$_{explicit}$ and SoA) using the R package *stats*. All results were corrected for multiple comparisons using the Bonferonni corrections

Thirdly, we tested the effect of gender of the avatar on the VR features and the BSC measurements. To do so, we ran two two-way repeated measures ANOVAs using the R package *rstatix* (Kassambara 2021). The first one tested for the main effects of Gender, VR features, and their interaction, while the second one tested the main effects of Gender, BSC measurements and interaction. Gender was composed of three categories ("Other", "Female", "Male"). The "Other" group was composed of 3 individuals, therefore we did not include it in our current analyses as it violates the assumption of normality. Additional analyses taking in account the "Other" group are presented in the supplementary section (**Table S6-S7**). All results were corrected for multiple comparisons using the Bonferonni corrections (adjusted p-values = 0.05/ 2= 0.025).

We then investigated the impact of VR experimental setup (HMD *versus* MRI-compatible goggle) on immersion. To do so, we ran a two-sample t-test between the immersion ratings of the group using the MRI-compatible goggle (Experiment 2, N = 29) and the rest of the sample using HMD (Experiments 3 & 4, N = 47).
Finally, we collected the spontaneous feedback on VR features, given by the participant at the end of each experiment. We grouped them into seven categories (skin tone, clothes, position, size, pixel, movement, and other) and quantified the number of feedback received for each category.

6.4 Results

First, we investigated how the participants rated the VR features. Mean, median, and standard deviation are presented in **Table 3,** while a detailed description per experiment is available in the supplementary section **Table S1-S4**.

Variable	# observations	Mean	Median	Sd
Age	102	24.787	24	3.827
Gender (O/F/M)	3/67/32			
Sense of agency (SoA)	102	0.661	0.72	0.236
Explicit Sense of ownership (SoO$_{Explicit}$)	102	0.515	0.512	0.269
Implicit Sense of ownership (SoO$_{Implicit}$)	102	0.308	0.191	0.293
Control for experimental bias	102	0.131	0.076	0.157
Resemblance	101	0.368	0.333	0.285
Immersion	77	0.53	0.5	0.29
Movement	102	0.6	0.667	0.259
Realism	102	0.557	0.5	0.25
Size	102	0.608	0.667	0.261
MRI-compatible goggle	29	28.4%		
HMD	73	71.6%		

Table 3. Descriptive statistics of the sample. Gender (O = other, F= female, M= male), HMD = Head-mounted display, Sd = standard deviation.

We found a significant main effect of the VR features (**Figure 2a**, $F_{(4, 304)}$ = 15.874, p <0.001). After Bonferroni corrections, *post-hoc* pairwise comparisons revealed that the main effect was driven by significantly lower ratings in avatar resemblance compared to the other VR features (adjusted p-values = 0.05/ 10= 0.005; resemblance – immersion: p = 0.007, resemblance – movement: p <0.0001, resemblance – realism: p <0.0001, resemblance – size: p <0.0001, see supplementary section **Table S5** for the detailed statistics).

In a second step, we quantified the relationship between VR features and BSC measurements. We first checked that SoA and SoO (both implicit and explicit measures) ratings were higher than ratings of items controlling for experimental bias (Q4 & Q5). We found a significant main effect of the repeated measure one-way ANOVA ($F_{(3,261)}$ = 131, p <0.0001). *post-hoc* pairwise comparisons confirmed that BSC measurements were higher than the control questions (see **Figure 2b** and **Table 4**).

Comparisons	Mean difference	Confidence interval (lower /upper)	df	p-value
Control-SoA	-0.53	-0.62 / -0.44	20.6	<0.0001
SoO_Explicit-SoA	-0.14	-0.23 / - 0.06	5.95	<0.0001
SoO_implicit-SoA	-0.35	-0.44 / - 0.26	10.1	<0.0001
SoO_Explicit- Control	0.38	0.29 / 0.47	14.2	<0.0001
SoO_implicit- Control	0.17	0.09 / 0.26	6.22	<0.0001
SoO_implicit-SoO_Explicit	-0.20	-0.30 /-0.11	6.85	<0.0001

Table 4. *Post-hoc pairwise comparisons between each pair of BSC measurements, p-value indicate significant threshold after Bonferonni correction (p-adjusted = 0.05/6 = 0.008). Significant correlations are indicated in bold. df = degree of freedom.*
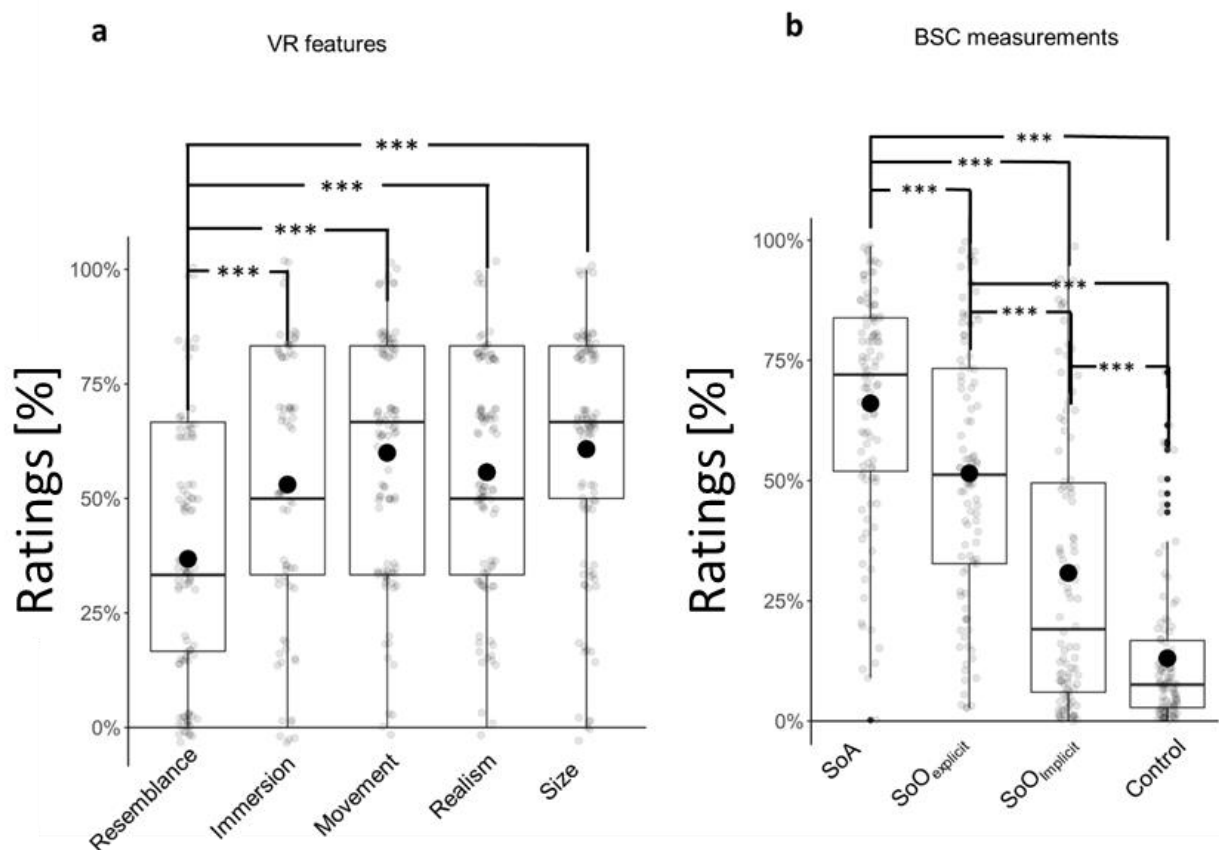

Figure 2. VR features and BSC measurements. a) *Ratings of avatar resemblance, immersion, realism of movement , realism of avatar and avatar size as rated in the four experiments. Avatar resemblance is rated significantly lower than the other four features as tested with a one-way ANOVA and post-hoc pairwise comparisons. N = 101, *** indicates significance level with p-value <0.001. Ratings are computed in percent with 100% corresponding to "totally agree" statement and 0% to "totally disagree" statement.* **b)** *Ratings of sense of agency (SoA), explicit sense of ownership (SoO_Explicit), implicit sense of ownership (SoO_implicit) and control questions. Control is rated significantly lower than the other three BSC measurements as tested with a one-way ANOVA and post-hoc pairwise comparisons. N = 102, *** indicates significance level with p-value <0.001. The lower and upper boundary of the box plot, indicate the 25th (Q1) and 75th (Q3) percentile respectively. The black line within the box indicate the median while the black dots within the box indicate the mean. The small grey dots indicate individual data point. Whiskers above and below the box indicate the minimum (Q1 − 1.5*IQR) and maximum (Q3 + 1.5*IQR) without the outliers. Small black dots outside of the whiskers indicates outliers. Ratings are computed in percent with 100% corresponding to "totally agree" statement and 0% to "totally disagree" statement.*

When we computed the correlations between the VR features and BSC measurements (see **Table 5**, the relationships which survived multiple comparisons corrections (adjusted p-values = 0.05/ 15= 0.003) were observed between the immersion and SoO$_{explicit}$ (r = 0.45, p <0.0001, **Figure 3a**) as well as between the size of the avatar and SoO$_{explicit}$ (r = 0.3, p = 0.002, **Figure 3b**).

Features	SoA		SoO$_{explicit}$		SoO$_{implicit}$	
	r	p-value	r	p-value	r	p-value
Resemblance	0.09	0.35	0.29	0.0034	0.28	0.004
Immersion	**0.14**	**0.21**	**0.45**	**<0.0001**	**0.25**	**0.03**
Movement	0.26	0.007	0.18	0.07	0.06	0.49
Realism	0.12	0.25	0.19	0.047	0.17	0.08
Size	**0.26**	**0.008**	**0.3**	**0.002**	**0.26**	**0.006**

Table 5. Comparison of BSC measurements. Post-hoc pairwise comparisons between each pair of BSC measurements, r indicates the Pearson correlation coefficient, and p-value indicates significant threshold after Bonferonni correction (p-adjusted = 0.05/15 = 0.0033). Significant correlations are indicated in bold. SoA = sense of agency, SoO$_{explicit}$ = explicit sense of ownership, SoO$_{implicit}$ = implicit sense of ownership.

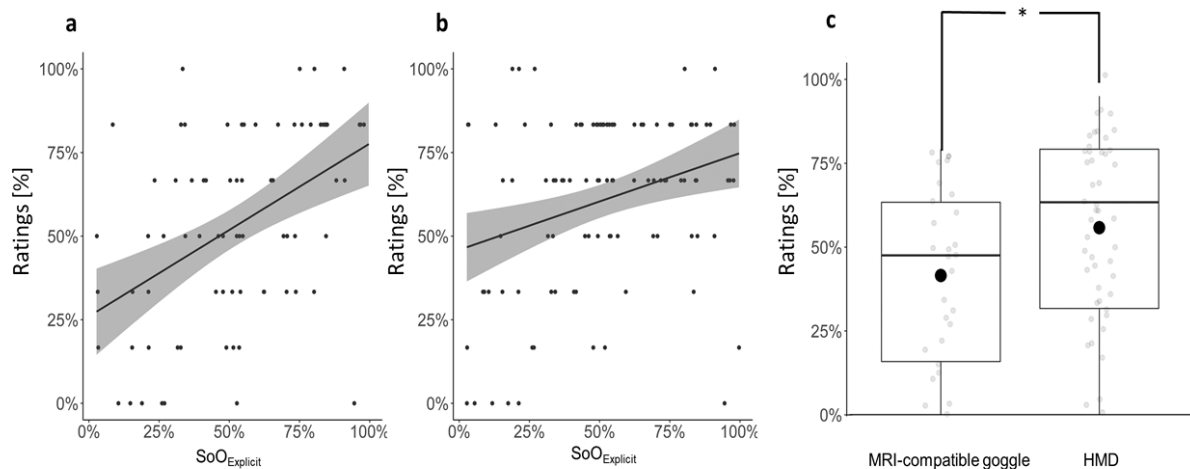*Figure 3. Stronger SoO is linked with immersion and avatar size. a) Positive correlation between SoO and immersion. SoO$_{Explicit}$ was positively related to the degree of immersion (r = 0.45, p <0.0001, N = 76). Ratings are computed in percent with 100% corresponding to "totally agree" statement and 0% to "totally disagree" statement. b) Positive correlation between SoO and avatar size. SoO$_{Explicit}$ was positively related to the avatar size (r = 0.3, p = 0.002). Ratings are computed in percent with 100% corresponding to "totally agree" statement and 0% to "totally disagree" statement. c). Stronger immersion with HMD. Immersion was higher when the VR scenario was observed with a head-mounted display (HMD) compared to when it was observed with MRI-compatible goggles. The lower and upper boundary of the box plot, indicate the 25th (Q1) and 75th (Q3) percentile respectively. The black line within the box indicate the median while the black dots within the box indicates the mean. The small grey dots indicate individual data point. Whiskers above and below the box indicate the minimum (Q1 − 1.5*IQR) and maximum (Q3 + 1.5*IQR) without the outliers. Ratings are computed in percent with 100% corresponding to "totally agree" statement and 0% to "totally disagree" statement.*

We then investigated if gender impacted VR features and BSC measurements as we used two avatars depending on the gender of participants (see **Figure 4**). We found no significant main effect of gender ($F_{(1,72)}$ = 0.59, p = 0.4) nor interaction on VR features ($F_{(4,288)}$ = 0.38, p = 0.8). The same analysis applied on BSC measurement did not show any significant main effect of gender ($F_{(1,97)}$ = 0.04, p= 0.8) nor interaction ($F_{(5,485)}$ = 1.03, p= 0.39).

Figure 4. Screenshot of the avatar used in this study. *The female avatar is on the left, and the male avatar is on the right. The experimenter chose the avatar's skin tone and gender to match each participant.*

Next, we investigated how the level of immersion of participants depended on the VR experimental setup used. We compared immersion ratings between participants wearing MRI-compatible goggle with participants immersed with HMD. As expected, the level of immersion was higher in the experiment with the HMD (**Figure 3c**, mean$_{\text{MRI-compatible goggles}}$ = 0.44, mean$_{\text{HMD}}$ = 0.59, $t_{58.89}$ = 2.26, p = 0.028).

Finally, we reported spontaneous feedback from participants (see **Table 6**). Most of the feedback was related to the avatar, specifically on the appearance (a total of 17 of the feedback concerned the skin tone, clothes and size) and on other avatar characteristics (realism of the movement and avatar position). It is noteworthy that we changed the skin tone of the avatar for 6 participants in total, among which 4 of them reported unmatched skin tone.

Features	Number of participants	Comments
Skin tone	4/100	Skin tone did not match (4)
Clothes	5/100	Clothes did not match (4), not enough detailed
Position	2/100	Avatar position was not realistic
Size	8/100	Avatar size was too small (3), too big(3), legs were too thin(1) too big (1)
Pixel	2/100	Scene was too "pixelized (1), look like a game (1)
Movement	7/100	Delay felt frustrating (2), as if there was a bug (3),not like in real life (2), was not noticed (1)
Other	2/100	No breathing animation (2), arm muscle too different (1)

Table 6. *Spontaneous feedback given by the participants on their VR experience. The number in parenthesis in the Comments column indicate the number of participants who gave feedback on the specific features*

6.5 Discussion

In this study, we investigated the effect of VR features from four experiments using VR and motion tracking as a tool to measure BSC. We found that SoO was related to the degree of participants' immersion in VR and the avatar's physical characteristics. Participants' spontaneous reports targeted mainly the physical characteristics of the avatar. Finally, we reported reduced immersion in the study using VR in MRI settings.

In this study, we observed low ratings regarding the avatar resemblance compared to the other VR features, suggesting that these features did not convince participants during their VR experience. This was further highlighted by the participants' spontaneous feedback, which mainly targeted the physical characteristics of the avatar regarding mismatch in avatar size, skin tone and avatar resemblance. This is in line with the literature, which outlines the importance of congruent skin tone and avatar size to ensure a suitable embodiment in VR (Fribourg et al., 2020; Jo et al., 2017; Waltemate et al., 2018). Notably, the spontaneous feedback on the skin tone was reported by participants for whom the avatar skin tone was changed, stressing the need for better rendering of different skin tones to improve VR experience. In the field of human cognition, physical characteristics can influence a variety of behavior from a change of distance perception linked to avatar size and realism (Banakou et al., 2013; Ogawa et al., 2018) to eating attitude change related to avatar size (Tambone et al., 2021). Therefore, our results indicate a need for amelioration in the avatar's physical characteristics to improve embodiment and presence during studies on BSC.

Moreover, the avatar's physical characteristics have been described to be correlated with SoO (Fribourg et al., 2020; Jo et al., 2017; Waltemate et al., 2018), emphasizing the necessity of matched physical characteristics to induce strong SoO. Our study corroborates these reports as we also observed a positive correlation between SoO and the avatar's size. Additionally, consistent with the literature, we found a positive correlation between immersion and SoO (Bowman & McMahan, 2007; Sanchez-Vives & Slate, 2005; Yuan & Steed, 2010). Interestingly, this link was specifically held with SoO and not SoA, indicating a dissociation between these two BSC components. Although SoO and SoA share similar characteristics (Pyasik et al., 2018), they do not require the same VR features. SoA is often immediately modulated by visuomotor synchronization of VR objects that do not necessarily look human (Imaizumi & Asai, 2015; Kilteni et al., 2012; Weijs et al., 2021). Conversely, SoO relies more on avatar characteristics; hence, the strength of bodily illusion might depend more on participants' overall VR experience (Jung & Lindeman, 2021; Meehan et al., 2002). However, in this study we used very stringent corrections for multiple comparisons, therefore, these corrections may hide the link between SoA and avatar physical characteristics. Application of Bayesian statistics might help disentangle the impact of VR features on SoA. Together, our results indicate that skin tone, clothes, and avatar size could be improved to better fit participants' appearance to enhance immersion and BSC, particularly, SoO.

Importantly, we did not find any significant effect of gender on the ratings of VR features and BSC measurements. This absence of significant effect is of interest as studies have revealed different relationships between avatar characteristics and user experience depending on gender. While men give more importance to the resemblance of the avatar, women are particularly attentive to body shape (Thaler et al., 2018) and avatar gender (Schwind et al., 2017). Our results suggest that the female and male avatars used in this study triggered similar ratings of VR features, suggesting that the VR experience was not different between gender. In our study, we had three gender non-conforming participants. To our knowledge, very few studies investigated the effect of immersion and embodiment in gender non-conforming participants. We found one study reporting that the use of more customizable avatars positively impacted the immersion and embodiment of gender non-conforming participants (Morgan et al., 2020). While our sample size did not allow us to perform statistical analysis regarding potential differences in their VR features ratings and BSC measurements compared to males and females, future studies should investigate such effects. Most importantly, creating an avatar with more neutral characteristics would benefit future studies to ensure a better immersion and induction of bodily illusions in participants.

To improve the overall physical characteristics of the avatar, some studies used body scan and augmented reality to get closer to the user's appearance (Brownridge & Twigg, 2014; Thaler et al., 2018). However, one can ask whether getting that close to user resemblance is necessary. Increasing avatar resemblance also increases the risk of falling into the uncanny valley (Geller, 2008; Mori et al., 2012). Studies have described that risk of getting into the uncanny valley was higher when using HMD compared to 2D screen (Hepperle et al., 2022). Our study showed that immersion was significantly reduced when VR was used in an MR-scanner with MRI-compatible goggles with reduced field of view and screen resolution. The degree of immersion is known to increase with larger field of view and screen resolution (Bowman & McMahan, 2007; North & North, 2016; Tan et al., 2006). In addition to the noisy environment related to the MR scanner, the participants could not move their head, a parameter which is known to contribute to immersion (Shu et al., 2019). To our knowledge, very few studies are using VR in MR-scanner as this technology is rather novel (Gauthier et al., 2021). However, we speculate that the combination of VR with MRI technology will increase in the next years with the constant increase of VR studies in human cognition (Pan & Hamilton, 2018). Our results point to the improvement of VR features for future research using VR in MR scanner, as it would contribute to counterbalancing the degree of immersion reduced in such kind of environment.

Our study highlight the importance of VR features and in particular immersion in the induction of bodily illusions. However, most VR studies disentangled between the term "*immersion*" defined as the technological characteristic (field of view, screen resolution) to trigger "*the sense of presence*", the subjective illusion which triggers ecological behavior in the virtual environment (North & North, 2016; Servotte et al., 2020). We did not disentangle between the two terms in our study because we were interested mainly by the participants' VR

experience, which relied on both immersion and sense of presence. Therefore a limitation of our study is that our results should be compared with caution with other studies discriminating between both terms.

In conclusion, this study underlines the effect of VR features on BSC measurements. We reported that SoO seems to be more impacted by VR features and physical characteristics of the avatar and accentuate the need to improve immersion for future studies using VR in highly disruptive environments such as MR scanner. Skin tone, avatar clothes and the development of gender-neutral avatars are the next VR features to improve to boost VR experience and the quality of our bodily illusion in the research field of BSC.

6.6 References

Arthur, K. W. (s. d.). *Effects of Field of View on Performance with Head-Mounted Displays*.

Banakou, D., Groten, R., & Slater, M. (2013). Illusory ownership of a virtual child body causes overestimation of object sizes and implicit
attitude changes. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(31), 12846-12851.
https://doi.org/10.1073/pnas.1306779110

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature Reviews Neuroscience*, *13*(8), Art. 8.
https://doi.org/10.1038/nrn3292

Blanke, O., Slater, M., & Serino, A. (2015). Behavioral, Neural, and Computational Principles of Bodily Self-Consciousness. *Neuron*, *88*(1),
145-166. https://doi.org/10.1016/j.neuron.2015.09.029

Botvinick. (1998). *Rubber hands 'feel' touch that eyes see | Nature*. https://www.nature.com/articles/35784

Bowman, D. A., & McMahan, R. P. (2007). Virtual Reality : How Much Immersion Is Enough? *Computer*, *40*(7), 36-43.
https://doi.org/10.1109/MC.2007.257

Brownridge, A., & Twigg, P. (2014). Body scanning for avatar production and animation. *International Journal of Fashion Design, Technology
and Education*, *7*(2), 125-132. https://doi.org/10.1080/17543266.2014.923049

Debarba, H. G., Bovet, S., Salomon, R., Blanke, O., Herbelin, B., & Boulic, R. (2017). Characterizing first and third person viewpoints and
their alternation for embodied interaction in virtual reality. *PLOS ONE*, *12*(12), e0190109.
https://doi.org/10.1371/journal.pone.0190109

Fribourg, R., Argelaguet, F., Lécuyer, A., & Hoyet, L. (2020). Avatar and Sense of Embodiment : Studying the Relative Preference Between
Appearance, Control and Point of View. *IEEE Transactions on Visualization and Computer Graphics*, *26*(5), 2062-2072.
https://doi.org/10.1109/TVCG.2020.2973077

Gauthier, B., Albert, L., Martuzzi, R., Herbelin, B., & Blanke, O. (2021). Virtual Reality platform for functional magnetic resonance imaging in
ecologically valid conditions. *Proceedings of the 27th ACM Symposium on Virtual Reality Software and Technology*, 1-12.
https://doi.org/10.1145/3489849.3489894

Geller, T. (2008). Overcoming the Uncanny Valley. *IEEE Computer Graphics and Applications*, *28*(4), 11-17.
https://doi.org/10.1109/MCG.2008.79

Gonzalez-Franco, M., & Lanier, J. (2017). Model of Illusions and Virtual Reality. *Frontiers in Psychology*, *8*.
https://www.frontiersin.org/articles/10.3389/fpsyg.2017.01125

Haggard, P. (2017). Sense of agency in the human brain. *Nature Reviews Neuroscience*, *18*(4), Art. 4. https://doi.org/10.1038/nrn.2017.14

Hepperle, D., Purps, C. F., Deuchler, J., & Wölfel, M. (2022). Aspects of visual avatar appearance : Self-representation, display type, and
uncanny valley. *The Visual Computer*, *38*(4), 1227-1244. https://doi.org/10.1007/s00371-021-02151-0

Imaizumi, S., & Asai, T. (2015). Dissociation of agency and body ownership following visuomotor temporal recalibration. *Frontiers in
Integrative Neuroscience*, *9*. https://www.frontiersin.org/articles/10.3389/fnint.2015.00035

Jo, D., Kim, K., Welch, G. F., Jeon, W., Kim, Y., Kim, K.-H., & Kim, G. J. (2017). The impact of avatar-owner visual similarity on body
ownership in immersive virtual reality. *Proceedings of the 23rd ACM Symposium on Virtual Reality Software and Technology*,
1-2. https://doi.org/10.1145/3139131.3141214

Jung, S., & Lindeman, Robert. W. (2021). Perspective : Does Realism Improve Presence in VR? Suggesting a Model and Metric for VR

Experience Evaluation. *Frontiers in Virtual Reality*, *2*. https://www.frontiersin.org/articles/10.3389/frvir.2021.693327

Kilteni, K., Groten, R., & Slater, M. (2012). The Sense of Embodiment in Virtual Reality. *Presence: Teleoperators and Virtual Environments*,

21(4), 373-387. https://doi.org/10.1162/PRES_a_00124

Kilteni, K., Maselli, A., Kording, K. P., & Slater, M. (2015). Over my fake body : Body ownership illusions for studying the multisensory basis

of own-body perception. *Frontiers in Human Neuroscience*, *9*, 141. https://doi.org/10.3389/fnhum.2015.00141

Lira, M., Egito, J. H., Dall'Agnol, P. A., Amodio, D. M., Gonçalves, Ó. F., & Boggio, P. S. (2017). The influence of skin colour on the experience

of ownership in the rubber hand illusion. *Scientific Reports*, *7*(1), Art. 1. https://doi.org/10.1038/s41598-017-16137-3

Meehan, M., Insko, B., Whitton, M., & Brooks, F. P. (2002). Physiological measures of presence in stressful virtual environments. *ACM

Transactions on Graphics*, *21*(3), 645-652. https://doi.org/10.1145/566654.566630

Morgan, H., O'Donovan, A., Almeida, R., Lin, A., & Perry, Y. (2020). The Role of the Avatar in Gaming for Trans and Gender Diverse Young

People. *International Journal of Environmental Research and Public Health*, *17*(22), 8617.

https://doi.org/10.3390/ijerph17228617

Mori, M., MacDorman, K. F., & Kageki, N. (2012). The Uncanny Valley [From the Field]. *IEEE Robotics & Automation Magazine*, *19*(2),

98-100. https://doi.org/10.1109/MRA.2012.2192811

North, M. M., & North, S. M. (2016). A Comparative Study of Sense of Presence of Traditional Virtual Reality and Immersive Environments.

Australasian Journal of Information Systems, *20*. https://doi.org/10.3127/ajis.v20i0.1168

Ogawa, N., Narumi, T., & Hirose, M. (2018). Object Size Perception in Immersive Virtual Reality : Avatar Realism Affects the Way We

Perceive. *2018 IEEE Conference on Virtual Reality and 3D User Interfaces (VR)*, 647-648.

https://doi.org/10.1109/VR.2018.8446318

Pan, X., & Hamilton, A. F. de C. (2018). Why and how to use virtual reality to study human social interaction : The challenges of exploring a

new research landscape. *British Journal of Psychology*, *109*(3), 395-417. https://doi.org/10.1111/bjop.12290

Pozeg, P., Galli, G., & Blanke, O. (2015). Those are Your Legs : The Effect of Visuo-Spatial Viewpoint on Visuo-Tactile Integration and Body

Ownership. *Frontiers in Psychology*, *6*. https://www.frontiersin.org/articles/10.3389/fpsyg.2015.01749

Pyasik, M., Burin, D., & Pia, L. (2018). On the relation between body ownership and sense of agency : A link at the level of sensory-related

signals. *Acta Psychologica*, *185*, 219-228. https://doi.org/10.1016/j.actpsy.2018.03.001

Sanchez-Vives & Slate. (2005). *From presence to consciousness through virtual reality | Nature Reviews Neuroscience*.

https://www.nature.com/articles/nrn1651

Schwind, V., Knierim, P., Tasci, C., Franczak, P., Haas, N., & Henze, N. (2017). « These are not my hands! » : Effect of Gender on the

Perception of Avatar Hands in Virtual Reality. *Proceedings of the 2017 CHI Conference on Human Factors in Computing Systems*,

1577-1582. https://doi.org/10.1145/3025453.3025602

Servotte, J.-C., Goosse, M., Campbell, S. H., Dardenne, N., Pilote, B., Simoneau, I. L., Guillaume, M., Bragard, I., & Ghuysen, A. (2020). Virtual

Reality Experience : Immersion, Sense of Presence, and Cybersickness. *Clinical Simulation in Nursing*, *38*, 35-43.

https://doi.org/10.1016/j.ecns.2019.09.006

Shu, Y., Huang, Y.-Z., Chang, S.-H., & Chen, M.-Y. (2019). Do virtual reality head-mounted displays make a difference? A comparison of presence and self-efficacy between head-mounted displays and desktop computer-facilitated virtual environments. *Virtual Reality*, *23*(4), 437-446. https://doi.org/10.1007/s10055-018-0376-x

Skurla, M. D., Rahman, A. T., Salcone, S., Mathias, L., Shah, B., Forester, B. P., & Vahia, I. V. (2022). Virtual reality and mental health in older adults : A systematic review. *International Psychogeriatrics*, *34*(2), 143-155. https://doi.org/10.1017/S104161022100017X

Slater et al. (2013). *Bystander responses to a violent incident in an immersive virtual environment—PubMed*. https://pubmed.ncbi.nlm.nih.gov/23300991/

Slater et al. (2022). *Encouraging bystander helping behaviour in a violent incident : A virtual reality study using reinforcement learning—PubMed*. https://pubmed.ncbi.nlm.nih.gov/35264652/

Tajadura-Jiménez, A., Banakou, D., Bianchi-Berthouze, N., & Slater, M. (2018). Author Correction : Embodiment in a Child-Like Talking Virtual Body Influences Object Size Perception, Self-Identification, and Subsequent Real Speaking. *Scientific Reports*, *8*(1), 4854. https://doi.org/10.1038/s41598-018-23231-7

Tambone, R., Poggio, G., Pyasik, M., Burin, D., Dal Monte, O., Schintu, S., Ciorli, T., Lucà, L., Semino, M. V., Doricchi, F., & Pia, L. (2021). Changing your body changes your eating attitudes : Embodiment of a slim virtual avatar induces avoidance of high-calorie food. *Heliyon*, *7*(7), e07515. https://doi.org/10.1016/j.heliyon.2021.e07515

Tan, D. S., Gergle, D., Scupelli, P., & Pausch, R. (2006). Physically large displays improve performance on spatial tasks. *ACM Transactions on Computer-Human Interaction*, *13*(1), 71-99. https://doi.org/10.1145/1143518.1143521

Thaler, A., Piryankova, I., Stefanucci, J. K., Pujades, S., de la Rosa, S., Streuber, S., Romero, J., Black, M. J., & Mohler, B. J. (2018). Visual Perception and Evaluation of Photo-Realistic Self-Avatars From 3D Body Scans in Males and Females. *Frontiers in ICT*, *5*. https://www.frontiersin.org/articles/10.3389/fict.2018.00018

Waltemate, T., Gall, D., Roth, D., Botsch, M., & Latoschik, M. E. (2018). The Impact of Avatar Personalization and Immersion on Virtual Body Ownership, Presence, and Emotional Response. *IEEE Transactions on Visualization and Computer Graphics*, *24*(4), 1643-1652. https://doi.org/10.1109/TVCG.2018.2794629

Weijs, M. L., Macartney, E., Daum, M. M., & Lenggenhager, B. (2021). Development of the bodily self : Effects of visuomotor synchrony and visual appearance on virtual embodiment in children and adults. *Journal of Experimental Child Psychology*, *210*, 105200. https://doi.org/10.1016/j.jecp.2021.105200

Yuan, Y., & Steed, A. (2010). Is the rubber hand illusion induced by immersive virtual reality? *2010 IEEE Virtual Reality Conference (VR)*, 95-102. https://doi.org/10.1109/VR.2010.5444807

Huntington-Klein N (2022). _vtable: Variable Table for Variable Documentation_. R package version 1.4.1, https://CRAN.R-project.org/package=vtable

Kassambara A (2021). _rstatix: Pipe-Friendly Framework for Basic Statistical Tests_. R package version 0.7.0, https://CRAN.R-project.org/package=rstatix.

Torsten Hothorn, Frank Bretz and Peter Westfall (2008). Simultaneous Inference in General Parametric Models. Biometrical Journal 50(3), 346--363

6.7 Supplementary Information
Table

Experiment 1				
Variable	**# observations**	**Mean**	**Median**	**Sd**
Age	26	22.739	22	3.387
Gender (O/F/M)	0/19/7			
Sense of agency (SoA)	26	0.613	0.648	0.256
Explicit Sense of ownership (SoO$_{Explicit}$)	26	0.47	0.471	0.297
Implicit Sense of ownership (SoO$_{Implicit}$)	26	0.249	0.127	0.277
Control for experimental bias	26	0.058	0.029	0.071
Resemblance	23	0.312	0.333	0.29
Immersion	*not assessed*			
Movement	24	0.431	0.333	0.207
Realism	24	0.521	0.5	0.222
Size	24	0.521	0.583	0.316

Table S1. Descriptive statistics of the sample for Experiment 1. *Gender (O = other, F= female, M= male), HMD = Head-mounted display, Sd = standard deviation.*

Experiment 2				
Variable	**# observations**	**Mean**	**Median**	**Sd**
Age	29	23.818	24	3.275
Gender (O/F/M)	3/16/10			
Sense of agency (SoA)	29	0.61	0.601	0.221
Explicit Sense of ownership (SoO$_{Explicit}$)	29	0.397	0.409	0.216
Implicit Sense of ownership (SoO$_{Implicit}$)	29	0.281	0.146	0.28
Control for experimental bias	29	0.16	0.08	0.18
Resemblance	29	0.339	0.333	0.283
Immersion	29	0.437	0.5	0.283
Movement	29	0.655	0.667	0.209
Realism	29	0.575	0.5	0.246
Size	29	0.598	0.667	0.246

Table S2. Descriptive statistics of the sample for Experiment 2. *Gender (O = other, F= female, M= male), HMD = Head-mounted display, Sd = standard deviation.*

Experiment 3				
Variable	# observations	Mean	Median	Sd
Age	24	27.292	27.50	3.689
Gender (O/F/M)	0/16/9			
Sense of agency (SoA)	24	0.694	0.763	0.229
Explicit Sense of ownership (SoO$_{Explicit}$)	24	0.611	0.604	0.246
Implicit Sense of ownership (SoO$_{Implicit}$)	24	0.407	0.369	0.292
Control for experimental bias	24	0.168	0.142	0.171
Resemblance	24	0.396	0.333	0.302
Immersion	24	0.638	0.667	0.283
Movement	24	0.625	0.667	0.283
Realism	24	0.5	0.5	0.315
Size	24	0.674	0.667	0.228

Table S3. Descriptive statistics of the sample for Experiment 3. Gender (O = other, F= female, M= male), HMD = Head-mounted display ,Sd = standard deviation.

Experiment 4				
Variable	# observations	Mean	Median	Sd
Age	26	25.120	24	3.539
Gender (O/F/M)	0/16/10			
Sense of agency (SoA)	26	0.734	0.76	0.23
Explicit Sense of ownership (SoO$_{Explicit}$)	26	0.604	0.624	0.267
Implicit Sense of ownership (SoO$_{Implicit}$)	26	0.301	0.118	0.319
Control for experimental bias	26	0.12	0.07	0.16
Resemblance	25	0.427	0.5	0.268
Immersion	25	0.54	0.5	0.278
Movement	25	0.673	0.667	0.274
Realism	25	0.627	0.667	0.2
Size	25	0.64	0.667	0.239

Table S4. Descriptive statistics of the sample for Experiment 4. Gender (O = other, F= female, M= male), HMD = Head-mounted display, Sd = standard deviation.

Pair of features	Mean difference	Confidence interval (lower/upper)	df	p-value
Immersion- Resemblance	**0.16**	**0.05/0.27**	**3.52**	**0.007**
Realism- Resemblance	**0.17**	**0.08/0.29**	**5.73**	**<0.0001**
Movement- Resemblance	**0.23**	**0.13/0.34**	**6.58**	**<0.0001**
Size- Resemblance	**0.24**	**0.14/0.34**	**8.26**	**<0.0001**
Movement-Immersion	0.07	-0.04/0.18	2.84	0.58
Realism-Immersion	0.03	-0.08/0.13	0.97	1
Size-Immersion	0.07	-0.03/0.18	2.55	0.12
Realism-Movement	-0.04	-0.15/0.06	-1.5	1
Size-Movement	0.008	-0.01/0.1	0.265	1
Size-Realism	0.05	-0.05/0.15	1.67	0.9

Table S5. Comparison of VR features. *Post-hoc pairwise comparisons applied with a Bonferroni correction on each pair of VR features to identify the significant difference between ratings. Avatar resemblance is significantly lower compared to the other VR features. Significant correlations are indicated in bold.*

Effect	dfn	dfd	F	p-value
Gender	2	74	2.16	0.12
VR features	**4**	**296**	**4.92**	**0.0007**
Gender * VR features	8	296	0.47	0.88

Table S6. Effect of gender on VR features. *Comparison of gender effect (3 factors: "Other"," Female"," Male") on VR features and their interaction. Significant correlations are indicated in bold. dfn = degree of freedom of numerator, dfd = degree of freedom of denominator.*

Effect	dfn	dfd	F	p-value
Gender	2	99	0.0008	0.9
BSC measurements	**5**	**495**	**32.89**	**<0.0001**
Gender * BSC measurements	10	495	0.69	0.73

Table S7. Effect of gender on BSC measurements. *Comparison of gender effect (3 factors: "Other"," Female"," Male") on BSC measurements and their interaction. Significant correlations are indicated in bold. dfn = degree of freedom of numerator, dfd = degree of freedom of denominator.*

7. General Discussion

In my thesis, I investigated the role of BSC and its subjective experience (especially SoA) during encoding process on EM and the related aspect of ANC. My work contributed to a better understanding of the relevance of self-consciousness, especially BSC as based on sensorimotor mechanisms, in EM. These different studies provided new insights into the behavioral, neural, and clinical mechanisms of BSC in EM. In this chapter, I will discuss the findings of the five studies included in this thesis and relate their results to the field of EM and BSC.

7.1 Summary of scientific contributions

The first part of my thesis focused on the impact of an experimental modulation of the SoA on the retrieval in EM (Study 1) and ANC (Study 2). The main results showed that hippocampal reinstatement reflects changes in BSC and further revealed hippocampal coupling with SoA-sensitive brain regions. Moreover, Study 1 showed that the EM performance and recollection were reduced under visuomotor and perspectival congruency for the amnestic patient with bilateral lesions in the hippocampal complex. Additionally, we found that ANC was positively correlated with SoA only under visuomotor and perspectival congruency, and this relation was neurally mediated by the functional connectivity between the right insula and the right mPFC, at encoding.

The second part of my thesis investigated the impact of the SoA, as manipulated by visuomotor and perspectival congruency more in-depth in clinical populations with lesions either in memory-related areas (Study 3) and in lesions affecting brain regions related to the sensorimotor aspect of BSC (Study 4). In Study 3, we reproduced the results found in the amnestic patient of Study 1 in two follow-up experiments: the patient had systematically a poorer recollection of events encoded under the embodied condition (preserved BSC). At the neural level, we found reduced functional connectivity between the bilateral hippocampus and parahippocampus and increased functional connectivity between mPFC and bilateral precuneus compared to age- and gender-match control. In Study 4, we found high variability in SoA sensitivity in stroke patients. We found slight changes in recognition performance depending on the patient's SoA sensitivity.

The third and last part of this thesis reflected on the technical-engineering aspects developed for Study 1 to 4 and presents ways of improving them (Study 5). Among the different VR features explored, the improvement should focus on more skin tone choices and better matching of avatar size, particularly for MRI studies, as immersion tends to be lowered in this type of environment.

7.2 Behavioral and neural correlates of bodily self-consciousness and episodic autobiographical memory

Behavioral correlates

More than fifty years ago, Rand and Wapner observed that EM depends on the body context (Rand & Wapner, 1967). Unfortunately, these findings did not receive the attention they deserved, and the investigation of the role of sensory bodily signals in EM remained scarce until the last decade. Since then, a few studies have demonstrated that a change of the perspective adopted at encoding and manipulation of the sense of ownership reduced EM and ANC (Bergouignan et al., 2014; Bréchet et al., 2019; Dijkstra et al., 2007; Gauthier et al., 2020; Iriye & Ehrsson, 2022). Our results in Study 1 showed that manipulation of SoA also impacts EM performance, as we found higher EM performance under visuomotor and perspectival congruency compared to the two conditions with visuomotor and perspectival incongruency. In Study 2, we linked the subjective experience related to the sensorimotor aspect of BSC (SoA) with ANC. We showed that when SoA was high, ANC was high but this effect was held only under visuomotor and perspectival congruency, that is, under preserved BSC. While previous work has shown that ANC depends on emotional arousal at encoding and retrieval (Kensinger & Ford, 2020; Neumann et al., 2007; Rimmele et al., 2011), this work provides new evidence that it also depends on sensorimotor processes and the SoA. This is in line with studies showing reduced recollection in schizophrenia patients (Corcoran & Frith, 2003; Neumann et al., 2007; Potheegadoo et al., 2013), who have been reported to have impairments in SoA and sensorimotor integration (Garbarini et al., 2016; Hauser et al., 2011; Jeannerod, 2009), which could thus explain their reduced ANC.

Surprisingly, the amnestic patient tested in Study 1 and Study 3 showed the opposite pattern between BSC and EM, suggesting that the hippocampal lesions or disconnection between the hippocampus and SoA regions in PMC and SMA altered the association between these two processes. In Study 1, we found a poorer recognition performance associated with a successful multisensory and sensorimotor integration (visuomotor and perspectival congruency) compared to the condition where the integration was altered (visuomotor and perspectival mismatch). Moreover, one week later, the patient could only retrieve the scene encoded in the condition with the normal multisensory and sensorimotor integration, indicating that events encoded in conditions with lower BSC facilitated retrieval. Our results in Study 3 reproduced these findings, as we found reduced recollection for scenes encoded under visuomotor and visuotactile congruency. These results can be interpreted in two-fold: First, it means that the patient did not have an EM performance enhanced by the visuomotor and perspectival congruency, as opposed to what was found in the experiment testing participants under intentional encoding in Study 1 and what is reported in the literature(Bergouignan et al., 2014; Bréchet et al., 2019; Dijkstra et al., 2007; Gauthier et al., 2020; Iriye & Ehrsson, 2022). Second, not only the EM performance was not enhanced, but in fact, it was lower compared

to the EM performance for scenes encoded under visuomotor and perspectival incongruency, as if the association between BSC and EM was disrupted in the patient.

While previous studies have reported a dissociation between EAM deficits and preserved cognitive self (De Renzi et al., 1997; Illman et al., 2011; S. B. Klein & Nichols, 2012; Levine et al., 1998, 2009), we showed in Study 1 and 3 that the patient had an EAM deficit but a preserved bodily self or BSC given that her sensitivity to our manipulation of SoA and body ownership were similar to that reported in healthy participants (Baier & Karnath, 2008; Lenggenhager et al., 2007; Padilla-Castañeda et al., 2014; Seghezzi, Giannini, et al., 2019; Weijs et al., 2021). In contrast, we reported altered sensitivity to the sensorimotor manipulation of BSC in some stroke patients with motor impairment tested in Study 4. While these results are preliminary and additional patients should be tested to draw robust conclusions, we found an absence of difference in the memory performance of patients with altered sensitivity to BSC.

Together, these results in healthy subjects and neurological patients show that EM depends on the sensory-motor body context as well as BSC. In the healthy brain, EM performance is enhanced, and EM recollection is stronger for events encoded under visuomotor and perspectival congruency. In the injured brain, when the hippocampus (and adjacent regions) are lesioned, BSC is dissociated from EM, and memory performance is diminished when scenes are encoded under visuomotor and perspectival congruency. Finally, when sensorimotor brain regions are lesioned, BSC is impaired, and the visuomotor congruency does not enhance memory performance.

BSC and the hippocampal-neocortical axis

At the neural level, EM has been linked with the hippocampus (Addis et al., 2004; Eldridge et al., 2005; Moser & Moser, 1998; Squire, 1992) and, more generally, to the medial temporal lobe (Eichenbaum et al., 2012; Squire et al., 2004). The reinstatement of hippocampal activity during the retrieval of episodic memories has been reported in several studies (Oedekoven et al., 2017; Pacheco Estefan et al., 2019; Tompary et al., 2016). Hippocampal reinstatement can be considered a neural proxy of successful memory because it is higher during successful retrieval than unsuccessful retrieval (Dupret et al., 2010; Liang & Preston, 2017; Tompary et al., 2016). Study 1 found similar results as the hippocampal reinstatement of participants correlated with their memory performance. Moreover, this relationship was confirmed even at the single trial level, where hippocampal reinstatement predicted memory performance per trial if the scenes presented were similar to the ones encoded. Study 1 demonstrated that hippocampal reinstatement was also sensitive to the BSC manipulation applied at encoding, suggesting that memory retrieval depends on the level of SoA at encoding. Therefore, from these results, we can infer that EM retrieval is mediated by hippocampal reinstatement, which is modulated by BSC states at encoding when encoding is associated with 1PP and when one's body is seen congruently with right hand movements.

Another possible explanation can be advanced regarding the reduced reinstatement observed under disrupted multisensory and sensorimotor integration in Study 1. Since the hippocampus

is at the top of the hierarchical organization of the medial temporal lobe (See Figure 2 in the general introduction; Lavenex & Amaral, 2000; Shimamura, 2010), it is possible that it receives only sensory signals that are highly integrated. In that case, the hippocampus would not have received the sensory signals while encoding the scene under visuomotor and perspectival incongruency. Similarly, As the patient could not retrieve EAM from events encoded before her infection, we could speculate that her lesions in the hippocampus and adjacent regions interfere with the hippocampal reinstatement necessary for the recollection of the episodic content.

However, in Study 1, despite decreased recognition performance under preserved BSC conditions, the patient performed above chance level for each condition, suggesting that she was able to perform the task despite her lesions. This suggests that EM recollection in the present task can also be independent of the hippocampus. Therefore, it is possible that the reinstatement of other regions in the medial temporal lobe, preserved in the patient, also enables the retrieval of EM content. In fact, a few studies report reinstatement of perirhinal cortex and parahippocampus during the retrieval of EM (Liang & Preston, 2017; Tompary et al., 2016).

Different regions of the medial temporal lobe have been involved in the retrieval of different types of memory content. For example, the retrieval of autobiographical memory was linked with increased functional connectivity between the hippocampus and parahippocampus, whereas the retrieval of general information and public events was linked with functional connectivity between the middle temporal gyrus and frontal pole (Maguire et al., 2000). In this regard, we could speculate that the encoding of a scene under visuomotor and perspectival congruency (and thus, preserved BSC state) is closer to autobiographical memory content. In contrast, scenes encoded under visuomotor and perspectival incongruency are less personal and relies on different neural substrates, independent on the hippocampus. Although purely speculative, this could also explain why the patient had a better recognition performance under visuomotor and perspectival incongruency.

Studies have also demonstrated cortical reinstatement during memory retrieval (Bosch et al., 2014; Gordon et al., 2014; Thakral et al., 2015; Wheeler, 2000). Moreover, recent evidence points towards a coupling between hippocampal reinstatement and sensory reactivation during EM retrieval (Nyberg et al., 2000; Pacheco Estefan et al., 2019; Ritchey et al., 2013; Sekeres et al., 2018). In Study 1, we found that the left dPMC and bilateral SMA were sensitive to our BSC manipulation. These brain regions are often cited as part of the neural correlates for sensorimotor aspects of BSC (Grivaz et al., 2017; Haggard, 2017). Critically, we found a coupling between the reinstatement of the hippocampus and the dPMC specific to the condition encoded under normal and highest multisensory and sensorimotor congruency. This suggests that the coupling of hippocampal reinstatement with the reactivation of sensory brain regions depends on BSC and body context at encoding. These results are consistent with the multiple trace theory (MTT) theory, in which the hippocampus indexes the information coming from the neocortex to retrieve EM (Moscovitch et al., 2016; Sekeres et al., 2017, 2018).

Interestingly, in Study 4, we found stronger autonoetic consciousness recollection for EAM encoded after motor stroke onset compared to before motor stroke onset. As the brain encounters a functional reorganization after stroke onset (Gandolla et al., 2021; Murphy & Corbett, 2009), this reorganization may impair the cortical reinstatement involved in EM recollection (Bosch et al., 2014; Gordon et al., 2014; Thakral et al., 2015; Wheeler, 2000). Therefore, we could explain the stronger autonoetic consciousness recollection by higher similarity between encoding and retrieval activity during recollection of EM after stroke onset.

Together, Studies 1 to 4 provide insight into how reinstatement mechanism mediates BSC and EM association in the healthy brain (Studies 1-2), with lesions in the hippocampus (Studies 1 and 3), and lesions in the cortex (Study 4).

7.3 Episodic memory engineering: how virtual reality and bodily self-consciousness bring us one step closer to episodic autobiographical memory

The main research question of this thesis was to understand how a subjective experience generated by the bodily context at encoding impacts the recollection of such events after long-term storage. Consequently, a principal interest was to mimick natural encoding conditions and test the memory of these events in delayed retrieval, attempting to be as close as possible to the processes involved in normal EM and EAM. Therefore, in most of this thesis, we used incidental encoding conditions as most of the events encoded in real life are encoded implicitly (Bjork et al., 1996). Furthermore, we used VR to give a richer context compared to the encoding of a list of words still used to test EM in clinics (Crossen et al., 1987; Smith, 2019). The use of VR for the investigation of EM enabled us to highlight deficits that were not measured in the classical way of testing EM using list of words (Plancher et al., 2008). The observation of natural behavior relies on immersion, VR realism and induction of SoA, and sense of ownership towards a virtual avatar (Fribourg et al., 2020; Jo et al., 2017; Waltemate et al., 2018). Our results in Studies 1 and 2 showed that our BSC manipulation worked, as participants had lower SoA under visuomotor and perspectival incongruency. This indicates that BSC encoded under visuomotor and perspectival congruency give rise to stronger subjective experience related to BSC, therefore getting closer to EAM under normal encoding conditions. Although we found lower immersion in the study in the MRI, we found a similar level of SoA and sense of ownership, suggesting that the subjective experience related to BSC induced by our immersive system was triggering the same strength of bodily illusions. Together, results of Study 5 imply that our VR system triggers relatively strong level of bodily illusion. For these reasons, we propose that our results can be extrapolated on EAM processes.

7.4 Limitations and future directions

The present thesis proposes to integrate BSC into the current MTT theory linking sensory information and EM. However, future work may also investigate differential effects of BSC manipulations on EM versus semantic memory.

First, the distinction between EM and semantic memory has its limitations. The dichotomy between these two memory systems has been discussed since their creation (De Brigard et al., 2022; Ratcliff & McKoon, 1986; Renoult et al., 2019), and more evidence tend to demonstrate that episodic and semantic memory retrieval also share common neural substrates (Irish & Vatansever, 2020). Therefore one could wonder why we focused explicitly on EM and not on the impact of BSC on semantic memory as well. As BSC generates a bodily-related subjective experience (Blanke, 2012; Tsakiris et al., 2010; Vignemont & Alsmith, 2017), it seems essential to understand how a subjective experience related to BSC affects the retrieval of memory in its specific *context*. Since the definition of EM is tightly linked to its encoding context (Tulving, 1972, 2002b), it was a good starting point for us to investigate the impact of the body context on memory. Moreover, as EM is tightly linked to the notion of the "self", particularly with ANC, we considered it more likely to be impacted by BSC than semantic memory.

Nevertheless, as the MTT states that semantic memory is stored in neocortical areas, the role of BSC and the related multisensory and sensorimotor integration might be relevant for this part of the memory (although it might affect retrieval and encoding processes in a different way compared to EM). Therefore, future studies should also investigate the potential effects of BSC on semantic memory. Moreover, the trace transformation theory (TTT), the updated version of MTT, also attributes different roles for the anterior and posterior hippocampus and different connections with the neocortex (Sekeres et al., 2017, 2018). Further studies with the amnestic patient of Studies 1 and 3 could thus test the effect of BSC on semantic memory and characterize the patient's lesions from Studies 1 and 3 using 7T MRI to provide insight into the specific partition of the hippocampus and how it mediates the BSC-EM and potential BSC-semantic association.

The present work focused mainly on BSC manipulation at encoding. Nevertheless, it is also relevant and possible to use the technology developed in this thesis to investigate how a change of bodily-related subjective experience at retrieval would impact the recollection of EM. As briefly discussed in Study 4, stroke patients and patients suffering from brain injuries are most likely a population for which the BSC state is altered at retrieval due to the stroke. The role of BSC at retrieval has mainly been investigated with perspective changes. Some studies have shown that the retrieval of EM from a 3PP reduced the strength of recollection of the memory (Bergouignan, 2021; Marcotti & St. Jacques, 2022). Future studies should manipulate different BSC components such as SoA and sense of ownership to understand better the effect of such manipulation on EM retrieval and their underlying neural mechanism.

Furthermore, this thesis did not dissociate the effect of specific bodily subjective experiences on EM. In other terms, we did not investigate the dissociation between the effect of SoA and sense of ownership on EM. Although SoA and sense of ownership both arise from the multisensory and sensorimotor integration of bodily signals and are tightly linked to BSC (Blanke, 2012; Blanke et al., 2015; Blanke & Metzinger, 2009), they also have distinct neural substrates and can be manipulated separately (Grivaz et al., 2017; Seghezzi, Giannini, et al., 2019; Tsakiris et al., 2010). Future studies should work closely on the neural difference between the effect of SoA and sense of ownership on EM.

Although it was not the main focus on the study, the data collected in Study 1 recorded the movement of the participants' right upper limb during the encoding of the virtual scenes. Therefore, a follow-up study could investigate the impact of motor involvement in EM. Do the participants have a better memory performance if they moved more their upper limb (and therefore get a stronger body context based on proprioceptive cues provided by their movement)? Additionally, we could relate these changes with the hippocampal reinstatement and further investigate whether the amount of movement during encoding is related to the activity of the motor cortex during retrieval.

The dissociation between BSC and EM found in the amnestic patient tested in Study 1 and 3 make us wonder whether the observed dissociation is mainly due to the lesions in the hippocampus themselves or to a disruption of functional connectivity between the hippocampus and BSC-related areas, such as the dPMC identified in Study 1 in healthy participants. This question is essential because the current work assumes that BSC network involves cortical areas and do not comprise the hippocampus. In that view, although the lesions could explain the absence of memory enhancement for scenes encoded under visuomotor and perspectival congruency in the amnestic patient, they are less likely to explain the diminution of memory performance under visuomotor and perspectival congruency compared to the manipulated BSC conditions. However, a few studies have discussed the role of the hippocampus in self-processes, notably in spatial representations of the self (Danjo et al., 2018; Gomez et al., 2012). As we did not record the brain activity of the patient during the task (due to the fact that we tested the patient in a different site than the healthy participants, where there was no possibility to perform the task in the MRI), we could not investigate whether the reinstatement between the hippocampus and dPMC was disrupted in the patient. Our next follow-up studies with the patient should tackle this question.

One methodological limitation of this thesis is its focus on static fMRI analysis to investigate how BSC impacts EM. It was necessary first to use a simple analysis to integrate BSC into the current EM framework. However, dynamic fMRI analysis should allow a better understanding of the neural mechanisms at stake during EM retrieval and their temporal relationships. One proposed line of research would be to apply a co-activation pattern analysis (CAPs) to investigate how the cortical areas and the areas of the medial temporal lobe are co-activated during encoding and retrieval processes.

Finally, on a long-term prospect, future studies should work on ways to integrate BSC into memory rehabilitation. Although rare, the case of the patient in Studies 1 and 3 is a perfect example of how such a project could benefit some patients. In the beginning of her recovery, the patient also lost all her personal history, including semantic autobiographical memory. But while she could relearn the semantic autobiographical memory, it has been (yet) impossible for her to relearn the subjective experience related to an EAM. Our results from Studies 1 and 3 suggest that recollection is at least more accessible when events are encoded under disrupted multisensory and sensorimotor integration. Could we imagine a setup to undergo such disruption in real life while she encodes meaningful personal events to enhance her recollection strength in a long-term goal? Future projects should work on that idea which could be further extended for other conditions with reduced EM retrieval (as in depression and schizophrenia; Jeannerod et al., 2009, Levine et al., 2014).

7.5 Conclusion

To conclude, the work presented in this thesis contributes to a better understanding of the role of BSC on EM and ANC. We showed that EM recollection depends on the sensorimotor aspect of BSC at encoding and its related subjective experience. For the first time, we provide empirical and imaging evidence to propose that BSC processes subscribe within the hippocampal-neocortical axis and the multiple trace theory. Specifically, BSC impacts the hippocampal reinstatement, a mechanism at the center of EM recollection and its related ANC. We further support our proposition by showing that recollection of episodic events encoded under preserved BSC is impaired in a patient with bilateral lesions in the hippocampus. Finally, we propose to study BSC and EM association within a cohort of motor stroke patients as their lesions impact the BSC system. Together, these findings open the door to deepening the investigation of the neural mechanism underpinning BSC and EM association. This could lead not only to a better understanding of the neural mechanisms involved in EM formation and retrieval but also to the development of new tools considering BSC for EM rehabilitation.

8. Annexes

8.1 Ongoing studies

During my thesis, I have been involved in several ongoing project. This section provides a brief description of each of these projects.

8.1.1 Focused ultrasound (FUS) to open the blood-brain barrier in the medial temporal lobe of patients with early Alzheimer's disease: FUS effects on spatial memory and neuroimaging

Contributions: data collection and analysis of fMRI data

In the last six months of my thesis, I had the opportunity to go to the Rockefeller Neuroscience Institute, West Virginia University (USA), thanks to the doc mobility grant awarded by EPFL. There, I tested the spatial memory of patients with early Alzheimer's disease who received a combined treatment of focus ultrasound (FUS) and antibody (Aduhelm) to decrease the reduction of amyloid beta plaque in their brain. FUS was applied unilaterally on targeted brain regions with a high accumulation of amyloid beta plaque as measured with a PET scan. Each patient received six treatments with a gradual increase in antibody (Aduhelm) dose. I tested three patients (total patients planned to be enrolled = 5) in a spatial memory task at baseline and after the second, fourth, and sixth treatments. Data collection and analysis are ongoing. Preliminary results indicate increased functional connectivity between the FUS-targeted regions (frontal areas) and posterior parietal regions (precuneus) specific to the targeted hemisphere (**Figure 1**). Spatial memory and functional activity during the task are not analyzed yet, as not enough patients and timepoint were collected.
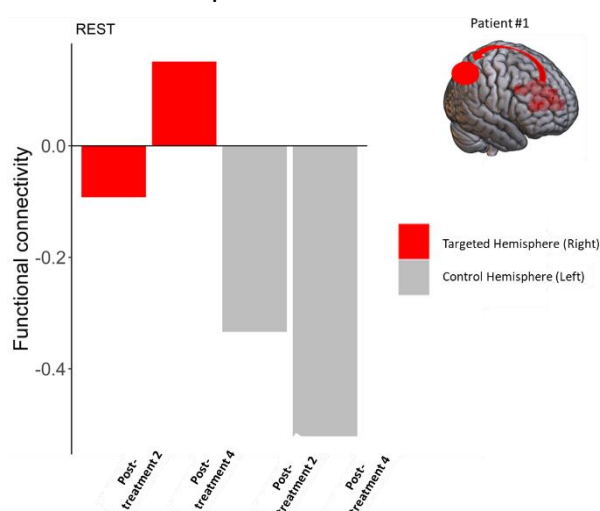

Figure 1. Functional connectivity at rest of one patient before and after FUS and Aduhelm treatment. *Functional connectivity at rest of one patient between the targeted zone of treatment with focus ultra sound (FUS), in frontal regions, and the parietal cortex. Targeted hemisphere is depicted in red (right hemisphere), non treated hemisphere is depicted in grey (left). No statistic were performed as each bar correspond to one datapoint. Results should be thus interpreted very cautiously.*

During the first part of my PhD, I worked mainly on body representation. I was involved in two projects, one investigating the longitudinal changes of body representation in stroke patients with upper limb motor impairment and the second one designing a rehabilitation tool using virtual reality to modulate upper limb representation. The pandemic slowed down these two projects heavily. The next sections (6.1.2 & 6.1.3) summarize these projects and their preliminary findings. The analysis is still ongoing.

8.1.2 Longitudinal investigation of body representation in stroke patients with motor impairment

Contributions: data collection and analysis of behavorial data

In collaboration with the UPHUMMEL lab (Prof. Friedhelm Hummel, EPFL), I participated to a longitudinal study (Towards Individualized Medecine in Stroke; TIMES) to assess biomarkers of motor recovery in stroke patients with upper limb motor impairement (Fleury et al., 2022). Patient undergo a large battery of tests including neuropsychological and motor tests, as well as MRI acquisition (resting-state and DWI), and TMS combined with EEG. The battery of tests was assessed one week, three weeks, three months, and twelve months after stroke. I conducted the data acquisition of the upper limb representation of stroke patients longitudinaly. Using the body-landmark task (Longo & Haggard 2010, Bassolino 2015), I tested the affected and unaffected upper limb representation of stroke patients at three weeks, three months and twelve months after stroke onset. This study aimed to understand how body representation was affected in stroke patients with motor impairment and how it evolved through time. Moreover, given the large amount of data collected for each patient, one specific goal was to understand how body representation evolved as a function of motor recovery. In total, more than 70 patients were tested. Preliminary results indicate that hand width was overestimated in all the patients and that this overestimation was reduced as a function of time. Ongoing analysis involve lesion mapping to link lesions location with body representation as well as resting-state functional connectivity analysis to better understand how to reorganization of brain function after stroke impacts body representation.

I would like to thank Michela Bassolino, who designed and implemented the task prior to the beginning of my PhD. She also collected the data of the last patients tested in this study during my stay at the Rockefeller Neuroscience Institute of West Virginia University.

8.1.3 Embodied virtual reality as a tool to rehabilitate upper limb representation: a proof-of-concept study in healthy population

Contributions: study design, data collection and analysis of behavorial data

In this project I used immersive virtual reality in young healthy participants to investigate the effect of the embodiment of a longer upper limb on body representation and movement kinematics. Participants embodied a virtual upper limb in two conditions (1) elongated conditions, in which the virtual upper limb was 1.5 times longer than their real hand, (2) standard conditions, in which the virtual task was matching their own hand size. After a brief embodiment session (cleaning virtual dust on a virtual table while holding a real sponge), participants were asked to observe a sphere placed at 80% of their maximum reaching distance. After a few seconds of observation, the sphere disappeared and participants had to reach to the location they think the sphere was. Wrist, elbow, shoulder and trunk positions were recorded. After 45 trials, participants upper limb representation was tested and compared with their baseline upper limb representation. This procedure was applied for each participant and each condition.

Preliminary results indicate a reduced reaching distance (**Figure 1A**), increased perceived arm length (**Figure 1B**) in the elongated condition.

These results provide promising insight to use virtual reality as a tool to rehabilitate upper limb representation in stroke patients.
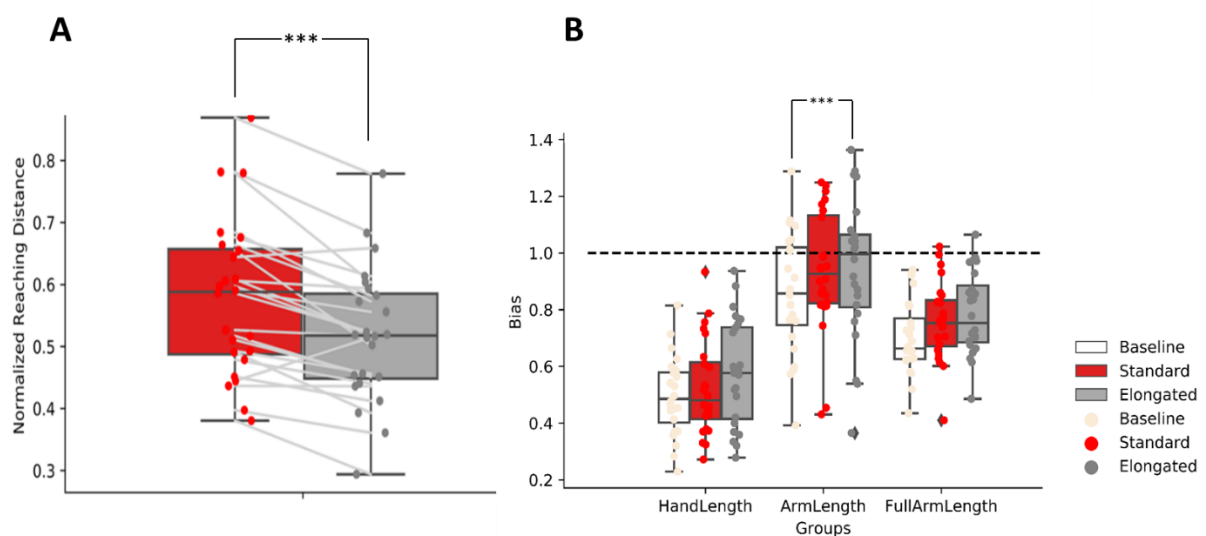
Manuscript is in preparation.

Figure 1. Main results. A. Reaching distance in virtual reality. *Distance crossed by the wrist in the standard (red) and elongated (grey) condition.****B. Upperlimb representation.*** *results of the bias of the upper limb dimension in the standard condition (red) and elongated condition (grey) for the hand length, arm length, and full arm length.*

9. Bibliography

Addis, D. R., Moscovitch, M., Crawley, A. P., & McAndrews, M. P. (2004). Recollective qualities modulate hippocampal activation during autobiographical memory retrieval. *Hippocampus*, *14*(6), 752-762. https://doi.org/10.1002/hipo.10215

Allé, M. C., Manning, L., Potheegadoo, J., Coutelle, R., Danion, J.-M., & Berna, F. (2017). Wearable Cameras Are Useful Tools to Investigate and Remediate Autobiographical Memory Impairment : A Systematic PRISMA Review. *Neuropsychology Review*, *27*(1), 81-99. https://doi.org/10.1007/s11065-016-9337-x

Allebone, J., Rayner, G., Siveges, B., & Wilson, S. J. (2015). Altered self-identity and autobiographical memory in epilepsy. *Epilepsia*, *56*(12), 1982-1991. https://doi.org/10.1111/epi.13215

Anderson, J. R., & Bower, G. H. (1972). Recognition and retrieval processes in free recall. *Psychological Review*, *79*, 97-123. https://doi.org/10.1037/h0033773

Andreano et al. (2009). *Auditory Cues Increase the Hippocampal Response to Unimodal Virtual Reality | CyberPsychology & Behavior*. https://www.liebertpub.com/doi/abs/10.1089/cpb.2009.0104

Baier, B., & Karnath, H.-O. (2008). Tight Link Between Our Sense of Limb Ownership and Self-Awareness of Actions. *Stroke*, *39*(2), 486-488. https://doi.org/10.1161/STROKEAHA.107.495606

Bergouignan. (2021). *Full article : Out-of-body memory encoding causes third-person perspective at recall*. https://www.tandfonline.com/doi/full/10.1080/20445911.2021.1958823

Bergouignan, L., Nyberg, L., & Ehrsson, H. H. (2014). Out-of-body–induced hippocampal amnesia. *Proceedings of the National Academy of Sciences*, *111*(12), 4421-4426. https://doi.org/10.1073/pnas.1318801111

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature Reviews Neuroscience*, *13*(8), Art. 8. https://doi.org/10.1038/nrn3292

Blanke, O., & Arzy, S. (2005). The Out-of-Body Experience : Disturbed Self-Processing at the Temporo-Parietal Junction. *The Neuroscientist*, *11*(1), 16-24. https://doi.org/10.1177/1073858404270885

Blanke, O., & Castillo, V. (Éds.). (2007). Clinical neuroimaging in epileptic patients with autoscopic hallucinations and out-of-body experiences. *Epileptologie*.

Blanke, O., & Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. *Trends in Cognitive Sciences*, *13*(1), 7-13. https://doi.org/10.1016/j.tics.2008.10.003

Blanke, O., & Mohr, C. (2005). Out-of-body experience, heautoscopy, and autoscopic hallucination of neurological origin : Implications for neurocognitive mechanisms of corporeal awareness and self-consciousness. *Brain Research Reviews*, *50*(1), 184-199. https://doi.org/10.1016/j.brainresrev.2005.05.008

Blanke, O., Slater, M., & Serino, A. (2015). Behavioral, Neural, and Computational Principles of Bodily Self-Consciousness. *Neuron*, *88*(1), 145-166. https://doi.org/10.1016/j.neuron.2015.09.029

Bosch, S. E., Jehee, J. F. M., Fernández, G., & Doeller, C. F. (2014). Reinstatement of Associative Memories in Early Visual Cortex Is Signaled by the Hippocampus. *Journal of Neuroscience*, *34*(22). https://doi.org/10.1523/JNEUROSCI.0805-14.2014

Botvinick & Cohen. (1998). *Rubber hands 'feel' touch that eyes see | Nature*. https://www.nature.com/articles/35784

Bréchet, L., Grivaz, P., Gauthier, B., & Blanke, O. (2018). Common Recruitment of Angular Gyrus in Episodic Autobiographical Memory and

   Bodily Self-Consciousness. *Frontiers in Behavioral Neuroscience*, *12*.

   https://www.frontiersin.org/articles/10.3389/fnbeh.2018.00270

Bréchet, L., Mange, R., Herbelin, B., Theillaud, Q., Gauthier, B., Serino, A., & Blanke, O. (2019). First-person view of one's body in immersive

   virtual reality : Influence on episodic memory. *PLOS ONE*, *14*(3), e0197763. https://doi.org/10.1371/journal.pone.0197763

Brunel, L., Labeye, E., Lesourd, M., & Versace, R. (2009). The sensory nature of episodic memory : Sensory priming effects due to memory

   trace activation. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *35*, 1081-1088.

   https://doi.org/10.1037/a0015537

Cabanis, M., Pyka, M., Mehl, S., Müller, B. W., Loos-Jankowiak, S., Winterer, G., Wölwer, W., Musso, F., Klingberg, S., Rapp, A. M., Langohr, K.,

   Wiedemann, G., Herrlich, J., Walter, H., Wagner, M., Schnell, K., Vogeley, K., Kockler, H., Shah, N. J., … Kircher, T. (2013). The

   precuneus and the insula in self-attributional processes. *Cognitive, Affective, & Behavioral Neuroscience*, *13*(2), 330-345.

   https://doi.org/10.3758/s13415-012-0143-5

Conway, A., Conway, M., Aggleton, J., & Conway, M. A. (2001). Sensory–perceptual episodic memory and its context : Autobiographical

   memory. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *356*(1413), 1375-1384.

   https://doi.org/10.1098/rstb.2001.0940

Corcoran, R., & Frith, C. D. (2003). Autobiographical memory and theory of mind : Evidence of a relationship in schizophrenia. *Psychological

   Medicine*, *33*(5), 897-905. https://doi.org/10.1017/S0033291703007529

Crossen et al. (1987). *Rey auditory-verbal learning test : Development of norms for healthy young adults : Clinical Neuropsychologist : Vol 2,

   No 1*. https://www.tandfonline.com/doi/abs/10.1080/13854048808520087

Cutsuridis, V., Cobb, S., & Graham, B. P. (2010). Encoding and retrieval in a model of the hippocampal CA1 microcircuit. *Hippocampus*, *20*(3),

   423-446. https://doi.org/10.1002/hipo.20661

Danjo, T., Toyoizumi, T., & Fujisawa, S. (2018). Spatial representations of self and other in the hippocampus. *Science*, *359*(6372), 213-218.

   https://doi.org/10.1126/science.aao3898

Danker, J. F., Tompary, A., & Davachi, L. (2017). Trial-by-Trial Hippocampal Encoding Activation Predicts the Fidelity of Cortical Reinstatement

   During Subsequent Retrieval. *Cerebral Cortex*, *27*(7), 3515-3524. https://doi.org/10.1093/cercor/bhw146

Davachi, L. (2006). Item, context and relational episodic encoding in humans. *Current Opinion in Neurobiology*, *16*(6), 693-700.

   https://doi.org/10.1016/j.conb.2006.10.012

David, N., Newen, A., & Vogeley, K. (2008). The "sense of agency" and its underlying cognitive and neural mechanisms. *Social Cognition,

   Emotion, and Self-Consciousness*, *17*(2), 523-534. https://doi.org/10.1016/j.concog.2008.03.004

Davis, E. T., Scott, K., Pair, J., Hodges, L. F., & Oliverio, J. (1999). Can Audio Enhance Visual Perception and Performance in a Virtual

   Environment? *Proceedings of the Human Factors and Ergonomics Society Annual Meeting*, *43*(22), 1197-1201.

   https://doi.org/10.1177/154193129904302206

De Brigard, F., Umanath, S., & Irish, M. (2022). Rethinking the distinction between episodic and semantic memory : Insights from the past,

   present, and future. *Memory & Cognition*, *50*(3), 459-463. https://doi.org/10.3758/s13421-022-01299-x

De Renzi, E., Lucchelli, F., Muggia, S., & Spinnler, H. (1997). Is memory loss without anatomical damage tantamount to a psychogenic deficit?

   The case of pure retrograde amnesia. *Neuropsychologia*, *35*(6), 781-794. https://doi.org/10.1016/S0028-3932(97)00018-3

Dere, E., Pause, B. M., & Pietrowsky, R. (2010). Emotion and episodic memory in neuropsychiatric disorders. *Behavioural Brain Research*, *215*(2), 162-171. https://doi.org/10.1016/j.bbr.2010.03.017

Dijkstra, K., Kaschak, M. P., & Zwaan, R. A. (2007). Body posture facilitates retrieval of autobiographical memories. *Cognition*, *102*(1), 139-149. https://doi.org/10.1016/j.cognition.2005.12.009

Dinh, H. Q., Walker, N., Hodges, L. F., Song, C., & Kobayashi, A. (1999). Evaluating the importance of multi-sensory input on memory and the sense of presence in virtual environments. *Proceedings IEEE Virtual Reality (Cat. No. 99CB36316)*, 222-228. https://doi.org/10.1109/VR.1999.756955

Dupret, D., O'Neill, J., Pleydell-Bouverie, B., & Csicsvari, J. (2010). The reorganization and reactivation of hippocampal maps predict spatial memory performance. *Nature Neuroscience*, *13*(8), Art. 8. https://doi.org/10.1038/nn.2599

Earhard, M. (1967). Cued recall and free recall as a function of the number of items per cue. *Journal of Verbal Learning and Verbal Behavior*, *6*(2), 257-263. https://doi.org/10.1016/S0022-5371(67)80105-1

Ehrsson, H. H. (2007). The Experimental Induction of Out-of-Body Experiences. *Science*, *317*(5841), 1048-1048. https://doi.org/10.1126/science.1142175

Eichenbaum, H., Sauvage, M., Fortin, N., Komorowski, R., & Lipton, P. (2012). Towards a functional organization of episodic memory in the medial temporal lobe. *Neuroscience & Biobehavioral Reviews*, *36*(7), 1597-1608. https://doi.org/10.1016/j.neubiorev.2011.07.006

Eichenbaum, H., Yonelinas, A. R., & Ranganath, C. (2007). The Medial Temporal Lobe and Recognition Memory. *Annual review of neuroscience*, *30*, 123-152. https://doi.org/10.1146/annurev.neuro.30.051606.094328

Eldridge, L. L., Engel, S. A., Zeineh, M. M., Bookheimer, S. Y., & Knowlton, B. J. (2005). A Dissociation of Encoding and Retrieval Processes in the Human Hippocampus. *Journal of Neuroscience*, *25*(13), 3280-3286. https://doi.org/10.1523/JNEUROSCI.3420-04.2005

Fanselow, M. S., & Dong, H.-W. (2010). Are the Dorsal and Ventral Hippocampus Functionally Distinct Structures? *Neuron*, *65*(1), 7-19. https://doi.org/10.1016/j.neuron.2009.11.031

Fletcher, P. C., Frith, C. D., Baker, S. C., Shallice, T., Frackowiak, R. S. J., & Dolan, R. J. (1995). The Mind's Eye—Precuneus Activation in Memory-Related Imagery. *NeuroImage*, *2*(3), 195-200. https://doi.org/10.1006/nimg.1995.1025

Freton, M., Lemogne, C., Bergouignan, L., Delaveau, P., Lehéricy, S., & Fossati, P. (2014). The eye of the self : Precuneus volume and visual perspective during autobiographical memory retrieval. *Brain Structure and Function*, *219*(3), 959-968. https://doi.org/10.1007/s00429-013-0546-2

Fribourg, R., Argelaguet, F., Lécuyer, A., & Hoyet, L. (2020). Avatar and Sense of Embodiment : Studying the Relative Preference Between Appearance, Control and Point of View. *IEEE Transactions on Visualization and Computer Graphics*, *26*(5), 2062-2072. https://doi.org/10.1109/TVCG.2020.2973077

Gallagher, S. (2000). Philosophical conceptions of the self : Implications for cognitive science. *Trends in Cognitive Sciences*, *4*(1), 14-21. https://doi.org/10.1016/S1364-6613(99)01417-5

Galvan Debarba, H., Boulic, R., Salomon, R., Blanke, O., & Herbelin, B. (2018). Self-attribution of distorted reaching movements in immersive virtual reality. *Computers & Graphics*, *76*, 142-152. https://doi.org/10.1016/j.cag.2018.09.001

Gamberini, L. (2000). Virtual Reality as a New Research Tool for the Study of Human Memory. *CyberPsychology & Behavior*, *3*(3), 337-342. https://doi.org/10.1089/10949310050078779

Gandolla, M., Niero, L., Molteni, F., Guanziroli, E., Ward, N. S., & Pedrocchi, A. (2021). Brain Plasticity Mechanisms Underlying Motor Control

Reorganization : Pilot Longitudinal Study on Post-Stroke Subjects. *Brain Sciences*, *11*(3), Art. 3.

https://doi.org/10.3390/brainsci11030329

Garbarini, F., Mastropasqua, A., Sigaudo, M., Rabuffetti, M., Piedimonte, A., Pia, L., & Rocca, P. (2016). Abnormal Sense of Agency in Patients

with Schizophrenia : Evidence from Bimanual Coupling Paradigm. *Frontiers in Behavioral Neuroscience*, *10*.

https://www.frontiersin.org/articles/10.3389/fnbeh.2016.00043

Gardiner, A., Conway, M., Aggleton, J., & Gardiner, J. M. (2001). Episodic memory and autonoetic consciousness : A first–person approach.

Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, *356*(1413), 1351-1361.

https://doi.org/10.1098/rstb.2001.0955

Gauthier, B., Bréchet, L., Lance, F., Mange, R., Herbelin, B., Faivre, N., Bolton, T. A. W., Ville, D. V. D., & Blanke, O. (2020). First-person body

view modulates the neural substrates of episodic memory and autonoetic consciousness : A functional connectivity study.

NeuroImage, *223*, 117370. https://doi.org/10.1016/j.neuroimage.2020.117370

Ghazanfar, A. A., & Schroeder, C. E. (2006). Is neocortex essentially multisensory? *Trends in Cognitive Sciences*, *10*(6), 278-285.

https://doi.org/10.1016/j.tics.2006.04.008

Gomez, A., Rousset, S., & Charnallet, A. (2012). Spatial deficits in an amnesic patient with hippocampal damage : Questioning the multiple

trace theory. *Hippocampus*, *22*(6), 1313-1324. https://doi.org/10.1002/hipo.20968

Gordon, A. M., Rissman, J., Kiani, R., & Wagner, A. D. (2014). Cortical Reinstatement Mediates the Relationship Between Content-Specific

Encoding Activity and Subsequent Recollection Decisions. *Cerebral Cortex*, *24*(12), 3350-3364.

https://doi.org/10.1093/cercor/bht194

Grivaz, P., Blanke, O., & Serino, A. (2017). Common and distinct brain regions processing multisensory bodily signals for peripersonal space

and body ownership. *NeuroImage*, *147*, 602-618. https://doi.org/10.1016/j.neuroimage.2016.12.052

Haering, C., & Kiesel, A. (2015). Was it me when it happened too early? Experience of delayed effects shapes sense of agency. *Cognition*, *136*,

38-42. https://doi.org/10.1016/j.cognition.2014.11.012

Haggard, P. (2017). Sense of agency in the human brain. *Nature Reviews Neuroscience*, *18*(4), Art. 4. https://doi.org/10.1038/nrn.2017.14

Haggard, P., & Chambon, V. (2012). Sense of agency. *Current Biology: CB*, *22*(10), R390-2.

Hamann, S. B., Ely, T. D., Grafton, S. T., & Kilts, C. D. (1999). Amygdala activity related to enhanced memory for pleasant and aversive stimuli.

Nature Neuroscience, *2*(3), Art. 3. https://doi.org/10.1038/6404

Hauser, M., Knoblich, G., Repp, B. H., Lautenschlager, M., Gallinat, J., Heinz, A., & Voss, M. (2011). Altered sense of agency in schizophrenia

and the putative psychotic prodrome. *Psychiatry Research*, *186*(2), 170-176. https://doi.org/10.1016/j.psychres.2010.08.003

Hodges, S., Berry, E., & Wood, K. (2011). SenseCam : A wearable camera that stimulates and rehabilitates autobiographical memory.

Memory, *19*(7), 685-696. https://doi.org/10.1080/09658211.2011.605591

Illman, N. A., Rathbone, C. J., Kemp, S., & Moulin, C. J. A. (2011). Autobiographical memory and the self in a case of transient epileptic

amnesia. *Epilepsy & Behavior*, *21*(1), 36-41. https://doi.org/10.1016/j.yebeh.2011.02.022

Irish. (2008). *Assessment of behavioural markers of autonoetic consciousness during episodic autobiographical memory retrieval : A

preliminary analysis—IOS Press*. https://content.iospress.com/articles/behavioural-neurology/ben00190

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

Irish, M., & Vatansever, D. (2020). Rethinking the episodic-semantic distinction from a gradient perspective. *Current Opinion in Behavioral Sciences*, *32*, 43-49. https://doi.org/10.1016/j.cobeha.2020.01.016

Iriye, H., & Ehrsson, H. H. (2022). Perceptual illusion of body-ownership within an immersive realistic environment enhances memory accuracy and re-experiencing. *IScience*, *25*(1), 103584. https://doi.org/10.1016/j.isci.2021.103584

Iriye, H., & Jacques, P. L. S. (2018). *Construction and Elaboration of Autobiographical Memories from Multiple Visual Perspectives* (p. 317594). bioRxiv. https://doi.org/10.1101/317594

Iriye, H., & St. Jacques, P. L. (2021). Memories for third-person experiences in immersive virtual reality. *Scientific Reports*, *11*(1), Art. 1. https://doi.org/10.1038/s41598-021-84047-6

Jeannerod, M. (2009). The sense of agency and its disturbances in schizophrenia : A reappraisal. *Experimental Brain Research*, *192*(3), 527-532. https://doi.org/10.1007/s00221-008-1533-3

Jo, D., Kim, K., Welch, G. F., Jeon, W., Kim, Y., Kim, K.-H., & Kim, G. J. (2017). The impact of avatar-owner visual similarity on body ownership in immersive virtual reality. *Proceedings of the 23rd ACM Symposium on Virtual Reality Software and Technology*, 1-2. https://doi.org/10.1145/3139131.3141214

Johnson, J., Suzuki, M., & Rugg, M. (2013). Recollection, familiarity, and content-sensitivity in lateral parietal cortex : A high-resolution fMRI study. *Frontiers in Human Neuroscience*, *7*. https://www.frontiersin.org/articles/10.3389/fnhum.2013.00219

Johnson, M. K., Foley, M. A., Suengas, A. G., & Raye, C. L. (1988). Phenomenal characteristics of memories for perceived and imagined autobiographical events. *Journal of Experimental Psychology: General*, *117*, 371-376. https://doi.org/10.1037/0096-3445.117.4.371

Kahn, I., Davachi, L., & Wagner, A. D. (2004). Functional-Neuroanatomic Correlates of Recollection : Implications for Models of Recognition Memory. *Journal of Neuroscience*, *24*(17), 4172-4180. https://doi.org/10.1523/JNEUROSCI.0624-04.2004

Kannape, O. A., & Blanke, O. (2013). Self in motion : Sensorimotor and cognitive mechanisms in gait agency. *Journal of Neurophysiology*, *110*(8), 1837-1847. https://doi.org/10.1152/jn.01042.2012

Kensinger, E. A., & Ford, J. H. (2020). Retrieval of Emotional Events from Memory. *Annual Review of Psychology*, *71*(1), 251-272. https://doi.org/10.1146/annurev-psych-010419-051123

Kesner, R. P. (1980). An attribute analysis of memory : The role of the hippocampus. *Physiological Psychology*, *8*(2), 189-197. https://doi.org/10.3758/BF03332850

Klein, S. B., & Nichols, S. (2012). Memory and the Sense of Personal Identity. *Mind*, *121*(483), 677-702. https://doi.org/10.1093/mind/fzs080

Krokos, E., Plaisant, C., & Varshney, A. (2019). Virtual memory palaces : Immersion aids recall. *Virtual Reality*, *23*(1), 1-15. https://doi.org/10.1007/s10055-018-0346-3

Lavenex, P., & Amaral, D. G. (2000). Hippocampal-neocortical interaction : A hierarchy of associativity. *Hippocampus*, *10*(4), 420-430. https://doi.org/10.1002/1098-1063(2000)10:4<420::AID-HIPO8>3.0.CO;2-5

Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video Ergo Sum : Manipulating Bodily Self-Consciousness. *Science*, *317*(5841), 1096-1099. https://doi.org/10.1126/science.1143439

Levine, B., Black, S. E., Cabeza, R., Sinden, M., Mcintosh, A. R., Toth, J. P., Tulving, E., & Stuss, D. T. (1998). Episodic memory and the self in a case of isolated retrograde amnesia. *Brain*, *121*(10), 1951-1973. https://doi.org/10.1093/brain/121.10.1951

Levine, B., Svoboda, E., Turner, G. R., Mandic, M., & Mackey, A. (2009). Behavioral and functional neuroanatomical correlates of anterograde autobiographical memory in isolated retrograde amnesic patient M.L. *Neuropsychologia*, *47*(11), 2188-2196. https://doi.org/10.1016/j.neuropsychologia.2008.12.026

Liang, J. C., & Preston, A. R. (2017). Medial temporal lobe reinstatement of content-specific details predicts source memory. *Cortex*, *91*, 67-78. https://doi.org/10.1016/j.cortex.2016.09.011

Linden, M. van der, Berkers, R. M. W. J., Morris, R. G. M., & Fernández, G. (2017). Angular Gyrus Involvement at Encoding and Retrieval Is Associated with Durable But Less Specific Memories. *Journal of Neuroscience*, *37*(39), 9474-9485. https://doi.org/10.1523/JNEUROSCI.3603-16.2017

Lum, J. A. G., & Conti-Ramsden, G. (2013). Long-term memory : A review and meta-analysis of studies of declarative and procedural memory in specific language impairment. *Topics in language disorders*, *33*(4), 282-297.

Lundstrom, B. N., Ingvar, M., & Petersson, K. M. (2005). The role of precuneus and left inferior frontal cortex during source memory episodic retrieval. *NeuroImage*, *27*(4), 824-834. https://doi.org/10.1016/j.neuroimage.2005.05.008

Maguire, E. A., Mummery, C. J., & Büchel, C. (2000). Patterns of hippocampal-cortical interaction dissociate temporal lobe memory subsystems. *Hippocampus*, *10*(4), 475-482. https://doi.org/10.1002/1098-1063(2000)10:4<475::AID-HIPO14>3.0.CO;2-X

Marcotti, P., & St. Jacques, P. L. (2022). Third-person perspectives in photographs influence visual and spatial perspectives during subsequent memory retrieval. *Journal of Cognitive Psychology*, *34*(1), 45-63. https://doi.org/10.1080/20445911.2021.1935972

Markowitsch, H. J., & Staniloiu, A. (2011). Memory, autonoetic consciousness, and the self. *Consciousness and Cognition*, *20*(1), 16-39. https://doi.org/10.1016/j.concog.2010.09.005

McCormick, C., Barry, D. N., Jafarian, A., Barnes, G. R., & Maguire, E. A. (2020). VmPFC Drives Hippocampal Processing during Autobiographical Memory Recall Regardless of Remoteness. *Cerebral Cortex*, *30*(11), 5972-5987. https://doi.org/10.1093/cercor/bhaa172

Moon, H.-J., Gauthier, B., Park, H.-D., Faivre, N., & Blanke, O. (2022). Sense of self impacts spatial navigation and hexadirectional coding in human entorhinal cortex. *Communications Biology*, *5*(1), Art. 1. https://doi.org/10.1038/s42003-022-03361-5

Moscovitch, M., Cabeza, R., Winocur, G., & Nadel, L. (2016). Episodic Memory and Beyond : The Hippocampus and Neocortex in Transformation. *Annual review of psychology*, *67*, 105-134. https://doi.org/10.1146/annurev-psych-113011-143733

Moser & Moser. (1998). *Functional differentiation in the hippocampus*. https://onlinelibrary.wiley.com/doi/abs/10.1002/(SICI)1098-1063(1998)8:6%3C608::AID-HIPO3%3E3.0.CO;2-7

Murphy, T. H., & Corbett, D. (2009). Plasticity during stroke recovery : From synapse to behaviour. *Nature Reviews Neuroscience*, *10*(12), Art. 12. https://doi.org/10.1038/nrn2735

Nadel, L., Samsonovich, A., Ryan, L., & Moscovitch, M. (2000). Multiple trace theory of human memory : Computational, neuroimaging, and neuropsychological results. *Hippocampus*, *10*(4), 352-368. https://doi.org/10.1002/1098-1063(2000)10:4<352::AID-HIPO2>3.0.CO;2-D

Neumann, A., Philippot, P., & Danion, J.-M. (2007). Impairment of Autonoetic Awareness for Emotional Events in Schizophrenia. *The Canadian Journal of Psychiatry*, *52*(7), 450-456. https://doi.org/10.1177/070674370705200707

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Nigro, G., & Neisser, U. (1983). Point of view in personal memories. *Cognitive Psychology*, *15*(4), 467-482. https://doi.org/10.1016/0010-0285(83)90016-6

Nyberg, L., Habib, R., McIntosh, A. R., & Tulving, E. (2000). Reactivation of encoding-related brain activity during memory retrieval. *Proceedings of the National Academy of Sciences*, *97*(20), 11120-11124. https://doi.org/10.1073/pnas.97.20.11120

Oedekoven, C. S. H., Keidel, J. L., Berens, S. C., & Bird, C. M. (2017). Reinstatement of memory representations for lifelike events over the course of a week. *Scientific Reports*, *7*(1), Art. 1. https://doi.org/10.1038/s41598-017-13938-4

Pacheco Estefan, D., Sánchez-Fibla, M., Duff, A., Principe, A., Rocamora, R., Zhang, H., Axmacher, N., & Verschure, P. F. M. J. (2019). Coordinated representational reinstatement in the human hippocampus and lateral temporal cortex during episodic memory retrieval. *Nature Communications*, *10*(1), Art. 1. https://doi.org/10.1038/s41467-019-09569-0

Padilla-Castañeda, M. A., Frisoli, A., Pabon, S., & Bergamasco, M. (2014). The Modulation of Ownership and Agency in the Virtual Hand Illusion under Visuotactile and Visuomotor Sensory Feedback. *Presence*, *23*(2), 209-225. https://doi.org/10.1162/PRES_a_00181

Pan, X., & Hamilton, A. F. de C. (2018). Why and how to use virtual reality to study human social interaction : The challenges of exploring a new research landscape. *British Journal of Psychology*, *109*(3), 395-417. https://doi.org/10.1111/bjop.12290

Park, H.-D., & Blanke, O. (2019). Coupling Inner and Outer Body for Self-Consciousness. *Trends in Cognitive Sciences*, *23*(5), 377-388. https://doi.org/10.1016/j.tics.2019.02.002

Pause, B., Zlomuzica, A., Kinugawa, K., Mariani, J., Pietrowsky, R., & Dere, E. (2013). Perspectives on Episodic-Like and Episodic Memory. *Frontiers in Behavioral Neuroscience*, *7*. https://www.frontiersin.org/articles/10.3389/fnbeh.2013.00033

Phelps, E. A. (2004). Human emotion and memory : Interactions of the amygdala and hippocampal complex. *Current Opinion in Neurobiology*, *14*(2), 198-202. https://doi.org/10.1016/j.conb.2004.03.015

Piolino, P., Desgranges, B., Belliard, S., Matuszewski, V., Lalevée, C., De La Sayette, V., & Eustache, F. (2003). Autobiographical memory and autonoetic consciousness : Triple dissociation in neurodegenerative diseases. *Brain*, *126*(10), 2203-2219. https://doi.org/10.1093/brain/awg222

Piolino, P., Desgranges, B., Clarys, D., Guillery-Girard, B., Taconnat, L., Isingrini, M., & Eustache, F. (2006). Autobiographical memory, autonoetic consciousness, and self-perspective in aging. *Psychology and Aging*, *21*(3), 510-525. https://doi.org/10.1037/0882-7974.21.3.510

Plancher, G., Barra, J., Orriols, E., & Piolino, P. (2013). The influence of action on episodic memory : A virtual reality study. *Quarterly Journal of Experimental Psychology*, *66*(5), 895-909. https://doi.org/10.1080/17470218.2012.722657

Plancher, G., Nicolas, S., & Piolino, P. (2008). Apport de la réalité virtuelle en neuropsychologie de la mémoire : Étude dans le vieillissement. *Psychologie & NeuroPsychiatrie du vieillissement*, *6*(1), 7-22. https://doi.org/10.1684/pnv.2008.0119

Potheegadoo, J., Berna, F., Cuervo-Lombard, C., & Danion, J.-M. (2013). Field visual perspective during autobiographical memory recall is less frequent among patients with schizophrenia. *Schizophrenia Research*, *150*(1), 88-92. https://doi.org/10.1016/j.schres.2013.07.035

Rand, G., & Wapner, S. (1967). Postural status as a factor in memory. *Journal of Verbal Learning and Verbal Behavior*, *6*(2), 268-271. https://doi.org/10.1016/S0022-5371(67)80107-5

Ratcliff, R., & McKoon, G. (1986). More on the distinction between episodic and semantic memories. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *12*, 312-313. https://doi.org/10.1037/0278-7393.12.2.312

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

Rimmele, U., Davachi, L., Petrov, R., Dougal, S., & Phelps, E. A. (2011). Emotion enhances the subjective feeling of remembering, despite lower accuracy for contextual details. *Emotion*, *11*, 553-562. https://doi.org/10.1037/a0024246

Ritchey, M., Wing, E. A., LaBar, K. S., & Cabeza, R. (2013). Neural Similarity Between Encoding and Retrieval is Related to Memory Via Hippocampal Interactions. *Cerebral Cortex*, *23*(12), 2818-2828. https://doi.org/10.1093/cercor/bhs258

Rosenbaum, R. S., Moscovitch, M., Foster, J. K., Schnyer, D. M., Gao, F., Kovacevic, N., Verfaellie, M., Black, S. E., & Levine, B. (2008). Patterns of Autobiographical Memory Loss in Medial-Temporal Lobe Amnesic Patients. *Journal of Cognitive Neuroscience*, *20*(8), 1490-1506. https://doi.org/10.1162/jocn.2008.20105

Rundus, D. (1971). Analysis of rehearsal processes in free recall. *Journal of Experimental Psychology*, *89*, 63-77. https://doi.org/10.1037/h0031185

Ryan, L., Nadel, L., Keil, K., Putnam, K., Schnyer, D., Trouard, T., & Moscovitch, M. (2001). Hippocampal complex and retrieval of recent and very remote autobiographical memories : Evidence from functional magnetic resonance imaging in neurologically intact people. *Hippocampus*, *11*(6), 707-714. https://doi.org/10.1002/hipo.1086

Sanchez-Vives & Slate. (2005). *From presence to consciousness through virtual reality | Nature Reviews Neuroscience*. https://www.nature.com/articles/nrn1651

Schacter, D. L., Guerin, S. A., & St. Jacques, P. L. (2011). Memory distortion : An adaptive perspective. *Trends in Cognitive Sciences*, *15*(10), 467-474. https://doi.org/10.1016/j.tics.2011.08.004

Seghezzi, S., Giannini, G., & Zapparoli, L. (2019). Neurofunctional correlates of body-ownership and sense of agency : A meta-analytical account of self-consciousness. *Cortex*, *121*, 169-178. https://doi.org/10.1016/j.cortex.2019.08.018

Seghezzi, S., Zirone, E., Paulesu, E., & Zapparoli, L. (2019). The Brain in (Willed) Action : A Meta-Analytical Comparison of Imaging Studies on Motor Intentionality and Sense of Agency. *Frontiers in Psychology*, *10*. https://www.frontiersin.org/articles/10.3389/fpsyg.2019.00804

Sekeres, M. J., Moscovitch, M., & Winocur, G. (2017). Mechanisms of Memory Consolidation and Transformation. In N. Axmacher & B. Rasch (Éds.), *Cognitive Neuroscience of Memory Consolidation* (p. 17-44). Springer International Publishing. https://doi.org/10.1007/978-3-319-45066-7_2

Sekeres, M. J., Winocur, G., & Moscovitch, M. (2018). The hippocampus and related neocortical structures in memory transformation. *Neuroscience Letters*, *680*, 39-53. https://doi.org/10.1016/j.neulet.2018.05.006

Shimamura, A. P. (2010). Hierarchical relational binding in the medial temporal lobe : The strong get stronger. *Hippocampus*, *20*(11), 1206-1216. https://doi.org/10.1002/hipo.20856

Shimamura, A. P., & Wickens, T. D. (2009). Superadditive memory strength for item and source recognition : The role of hierarchical relational binding in the medial temporal lobe. *Psychological Review*, *116*, 1-19. https://doi.org/10.1037/a0014500

Skurla, M. D., Rahman, A. T., Salcone, S., Mathias, L., Shah, B., Forester, B. P., & Vahia, I. V. (2022). Virtual reality and mental health in older adults : A systematic review. *International Psychogeriatrics*, *34*(2), 143-155. https://doi.org/10.1017/S104161022100017X

Smith, S. A. (2019). Virtual reality in episodic memory research : A review. *Psychonomic Bulletin & Review*, *26*(4), 1213-1237. https://doi.org/10.3758/s13423-019-01605-w

Sorokowska, A., Nord, M., Stefańczyk, M. M., & Larsson, M. (2022). Odor-based context-dependent memory : Influence of olfactory cues on declarative and nondeclarative memory indices. *Learning & Memory*, *29*(5), 136-141. https://doi.org/10.1101/lm.053562.121

Squire, L. R. (1992). Memory and the hippocampus : A synthesis from findings with rats, monkeys, and humans. *Psychological Review*, *99*, 195-231. https://doi.org/10.1037/0033-295X.99.2.195

Squire, L. R., Stark, C. E. L., & Clark, R. E. (2004). The Medial Temporal Lobe. *Annual Review of Neuroscience*, *27*(1), 279-306. https://doi.org/10.1146/annurev.neuro.27.070203.144130

St. Jacques, P. L. (2019). A New Perspective on Visual Perspective in Memory. *Current Directions in Psychological Science*, *28*(5), 450-455. https://doi.org/10.1177/0963721419850158

St. Jacques, P. L., & Schacter, D. L. (2013). Modifying Memory : Selectively Enhancing and Updating Personal Memories for a Museum Tour by Reactivating Them. *Psychological Science*, *24*(4), 537-543. https://doi.org/10.1177/0956797612457377

St. Jacques, P. L., Szpunar, K. K., & Schacter, D. L. (2017). Shifting visual perspective during retrieval shapes autobiographical memories. *NeuroImage*, *148*, 103-114. https://doi.org/10.1016/j.neuroimage.2016.12.028

Staresina, B. P., Cooper, E., & Henson, R. N. (2013). Reversible Information Flow across the Medial Temporal Lobe : The Hippocampus Links Cortical Modules during Memory Retrieval. *Journal of Neuroscience*, *33*(35), 14184-14192. https://doi.org/10.1523/JNEUROSCI.1987-13.2013

Summerfield, C., Greene, M., Wager, T., Egner, T., Hirsch, J., & Mangels, J. (2006). Neocortical Connectivity during Episodic Memory Formation. *PLOS Biology*, *4*(5), e128. https://doi.org/10.1371/journal.pbio.0040128

Thakral, P. P., Wang, T. H., & Rugg, M. D. (2015). Cortical reinstatement and the confidence and accuracy of source memory. *NeuroImage*, *109*, 118-129. https://doi.org/10.1016/j.neuroimage.2015.01.003

Tompary, A., Duncan, K., & Davachi, L. (2016). High-resolution investigation of memory-specific reinstatement in the hippocampus and perirhinal cortex. *Hippocampus*, *26*(8), 995-1007. https://doi.org/10.1002/hipo.22582

Tortell et al. (2007). *The effects of scent and game play experience on memory of a virtual environment | SpringerLink*. https://link.springer.com/article/10.1007/s10055-006-0056-0

Trimble, M. R., & Cavanna, A. E. (2008). Chapter 3.7 The role of the precuneus in episodic memory. In E. Dere, A. Easton, L. Nadel, & J. P. Huston (Éds.), *Handbook of Behavioral Neuroscience* (Vol. 18, p. 363-377). Elsevier. https://doi.org/10.1016/S1569-7339(08)00220-8

Tsakiris, M., Longo, M. R., & Haggard, P. (2010). Having a body versus moving your body : Neural signatures of agency and body-ownership. *Neuropsychologia*, *48*(9), 2740-2749. https://doi.org/10.1016/j.neuropsychologia.2010.05.021

Tulving, E. (1972). Episodic and semantic memory. In *Organization of memory* (p. xiii, 423-xiii, 423). Academic Press.

Tulving, E. (1985). Memory and consciousness. *Canadian Psychology / Psychologie canadienne*, *26*, 1-12. https://doi.org/10.1037/h0080017

Tulving, E. (2002). Episodic Memory : From Mind to Brain. *Annual Review of Psychology*, *53*(1), 1-25. https://doi.org/10.1146/annurev.psych.53.100901.135114

Tulving, E., & Osler, S. (1968). Effectiveness of retrieval cues in memory for words. *Journal of Experimental Psychology*, *77*, 593-601. https://doi.org/10.1037/h0026069

Tulving, E., & Wiseman, S. (1975). Relation between recognition and recognition failure of recallable words. *Bulletin of the Psychonomic Society*, *6*(1), 79-82. https://doi.org/10.3758/BF03333153

Turk-Browne, N. B. (2019). The hippocampus as a visual area organized by space and time : A spatiotemporal similarity hypothesis. *Vision Research*, *165*, 123-130. https://doi.org/10.1016/j.visres.2019.10.007

Waltemate, T., Gall, D., Roth, D., Botsch, M., & Latoschik, M. E. (2018). The Impact of Avatar Personalization and Immersion on Virtual Body Ownership, Presence, and Emotional Response. *IEEE Transactions on Visualization and Computer Graphics*, *24*(4), 1643-1652. https://doi.org/10.1109/TVCG.2018.2794629

Weijs, M. L., Macartney, E., Daum, M. M., & Lenggenhager, B. (2021). Development of the bodily self : Effects of visuomotor synchrony and visual appearance on virtual embodiment in children and adults. *Journal of Experimental Child Psychology*, *210*, 105200. https://doi.org/10.1016/j.jecp.2021.105200

Wheeler. (2000). *Memory's echo : Vivid remembering reactivates sensory-specific cortex | PNAS*. https://www.pnas.org/doi/abs/10.1073/pnas.97.20.11125

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

Wheeler, M. E., & Buckner, R. L. (2004). Functional-anatomic correlates of remembering and knowing. *NeuroImage*, *21*(4), 1337-1349. https://doi.org/10.1016/j.neuroimage.2003.11.001

Winocur, G., & Moscovitch, M. (2011). Memory Transformation and Systems Consolidation. *Journal of the International Neuropsychological Society*, *17*(5), 766-780. https://doi.org/10.1017/S1355617711000683

Woodruff, C. C., Johnson, J. D., Uncapher, M. R., & Rugg, M. D. (2005). Content-specificity of the neural correlates of recollection. *Neuropsychologia*, *43*(7), 1022-1032. https://doi.org/10.1016/j.neuropsychologia.2004.10.013

Xiao, X., Dong, Q., Gao, J., Men, W., Poldrack, R. A., & Xue, G. (2017). Transformed Neural Pattern Reinstatement during Episodic Memory Retrieval. *Journal of Neuroscience*, *37*(11), 2986-2998. https://doi.org/10.1523/JNEUROSCI.2324-16.2017

Zito, G. A., Wiest, R., & Aybek, S. (2020). Neural correlates of sense of agency in motor control : A neuroimaging meta-analysis. *PLOS ONE*, *15*(6), e0234321. https://doi.org/10.1371/journal.pone.0234321

10. Curriculum Vitae

NATHALIE HEIDI MEYER

Ph.D. candidate in cognitive neuroscience

Engineer in Life Sciences and Technology

CONTACT DETAILS

Address: Pl.Tunnel 3 1005 Lausanne
Email: nathalie.meyer@epfl.ch
Phone: +41796902219
LinkedIn:
https://www.linkedin.com/in/nathalie-heidi-meyer/

KEY SKILLS

Data analysis, experiment with clinical population, good clinical practice, virtual reality, functional magnetic resonance imaging acquisition and analysis - task based and connectivity, Statistics

SOFT SKILLS

Organized
Solution-oriented
Independant
Dynamic
Efficient time manager
Team spirited

PROGRAMMING SKILLS & TOOLS

Matlab, SPM, conn toolbox
Python,pandas, numpy matplotlib
C++
C#, Unity
R,RStudio
FSL

LANGUAGE

French - mother tongue
English - fluent
German - basic
Mandarin - basic (spoken)

INTERESTS

Hiking, dansing, chess, travel-adventures, running & swimming

CAREER

Ph.D student in Cognitive neuroscience

Laboratory of cognitive neuroscience Swiss Federal Institute of Technology (EPFL) | Sept 2018 -Present

Experimental design and execution; Data analysis: behavioral and fMRI; Data interpretation; scientific communication & writing;

Doc Mobility grant from EPFL: Focused ultrasound (FUS) to open the blood-brain barrier in the medial temporal lobe of patients with early Alzheimer's disease: FUS effects on spatial memory and neuroimaging at **the Rockefeller Neurosciences Institute of West Virginia University (USA)**

Research Assistant

Laboratory of Behavioral Genetics Swiss Federal Institute of Technology (EPFL) | March 2018 -June 2018

Data collection in healthy participants. Virtual reality; Motion tracking; EEG

Master thesis

Laboratory of Cerebral Disease Donders Institute , The Netherlands | August 2017 -January 2018

Longitudinal resting-state fMRI analysis; patients with small vessel disease; voxel-lesion symptom mapping;

EDUCATION

Sept 2018 -Present   Ph.D in Cognitive neuroscience

Laboratory of cognitive neuroscience Swiss Federal Institute of Technology (EPFL)

Sept 2015 - January 2018 MSc in Life Sciences and Technologies (specialization in neurosciences)

Swiss Federal Institute of Technology (EPFL) |

Sept 2012 - July 2015 BSc in Life Sciences and Technologies

Swiss Federal Institute of Technology (EPFL) |

Sept 2009 - July 2012 Swiss Matura

Gymnase de Chamblandes |

PUBLICATIONS

Fleury et al., (2022) Towards individualized Medicine in Stroke – the TiMeS project: protocol of longitudinal, multi-modal, multi-domain study in stroke **Frontiers in Neurology** 15th author: Data collection

Camerino, I. et al., (2020) White matter hyperintensies and verbal fluency **Human Brain Mapping** 4th author: Voxel-lesion symptom mapping

Rodrigues, J. et al., (2020) Locomotion as a predictor of stress **Nature communications** 4th author: Data collection