NeuroImage 223 (2020) 117370

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage

First-person body view modulates the neural substrates of episodic memory and autonoetic consciousness: A functional connectivity study

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ARTICLE INFO

Keywords:
Episodic memory
Virtual reality
Bodily self-consciousness
Resting-state functional connectivity
Autonoetic consciousness

ABSTRACT

Episodic memory (EM) is classically conceived as a memory for events, localized in space and time, and characterized by autonoetic consciousness (ANC) allowing to mentally travel back in time and subjectively relive an event. Building on recent evidence that the first-person visual co-perception of one's own body during encoding impacts EM, we used a scene recognition task in immersive virtual reality (VR) and measured how first-person body view would modulate peri-encoding resting-state fMRI, EM performance, and ANC. Specifically, we investigated the impact of body view on post-encoding functional connectivity in an *a priori* network of regions related either to EM or multisensory bodily processing and used these regions in a seed-to-whole brain analysis. Post-encoding connectivity between right hippocampus (rHC) and right parahippocampus (rPHC) was enhanced when participants encoded scenes while seeing their body. Moreover, the strength of connectivity between the rHC, rPHC and the neocortex displayed two main patterns with respect to body view. The connectivity with a sensorimotor fronto-parietal network, comprising primary somatosensory and primary motor cortices, correlated with ANC after - but not before - encoding, depending on body view. The opposite change of connectivity was found between rHC, rPHC and the medial parietal cortex (from being correlated with ANC before encoding to an absence of correlation after encoding), but irrespective of body view. Linking immersive VR and fMRI for the study of EM and ANC, these findings suggest that seeing one's own body during encoding impacts the brain activity related to EM formation by modulating the connectivity between the right hippocampal formation and the neocortical regions involved in the processing of multisensory bodily signals and self-consciousness.

1. Introduction

Episodic memory (EM) is a form of long-term memory characterized by the embedding of encoded events within a specific context and by autonoetic consciousness (ANC) (Gardiner, 2001; Tulving, 1985; Wheeler et al., 1997). Tulving postulated that ANC is a form of self-consciousness allowing the representation of oneself in subjective time, extending from the past to the future, and associated with EM retrieval. Specifically, remembering events in EM is associated with the subjective experience of mentally travelling back in time and re-experiencing a past event within its spatiotemporal context (Tulving, 2002, 1985). As EM recall involves regaining knowledge of the content of a past event as well as the self-conscious (or autonoetic) experience of reliving this event, we hypothesize that manipulating multisensory signals that impact self-consciousness during the encoding of events would modify EM formation and specifically ANC during recall.

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https://doi.org/10.1016/j.neuroimage.2020.117370
Received 19 May 2020; Received in revised form 26 August 2020; Accepted 8 September 2020
Available online 12 September 2020

Recently, self-consciousness has been approached experimentally by studying an embodied or bodily component of self-consciousness (bodily self-consciousness, BSC) (Blanke, 2012; Blanke et al., 2015; Ehrsson, 2007; Tsakiris, 2010) and shown to be of relevance for EM (Bergouignan et al., 2014; Bréchet et al., 2020, 2019, 2018). BSC is based on the integration of exteroceptive and interoceptive multisensory inputs (Apps et al., 2012; Botvinick and Cohen, 1998; De Vignemont, 2011; Ehrsson, 2007, 2004; Ionta et al., 2011; Jeannerod, 2007; Lenggenhager et al., 2007) and includes major bodily components like self-identification, self-location and first-person perspective (Blanke, 2012; Blanke et al., 2015). Several recent lines of evidence indicate that BSC and EM are linked by common cognitive processes. First, EM retrieval involves different forms of perspective taking such as field perspective and observer perspective (Freton et al., 2014; Jacques et al., 2016; Marcotti and St. Jacques, 2018; Rubin and Umanath, 2015), which share many aspects with third and first-person perspective taking employed in social neuroscience and BSC research. Specifically, it has been shown that perspective taking modulates memory performance (St. Jacques et al., 2016; Marcotti and St. Jacques, 2018) as well as subjective aspects of EM (Bergouignan et al., 2014). Second, there is evidence that self-identification impairments (a component of BSC; Blanke et al., 2015) in elderly healthy humans and patients with Alzheimer's disease are related to deficits in EM for autobiographical events (Addis and Tippett, 2004; El Haj et al., 2015). Third, BSC and EM share multisensory mechanisms (Rothschild, 2019). Taken together, these empirical findings suggest that EM involves the naturalistic viewing of one's own body during encoding (i.e., the co-perception of one's body and the world from the first-person perspective). Recently, we brought new evidence in favor of this view by showing, with a new paradigm for EM research based on immersive virtual reality (VR), that body-related visual signals known to modulate BSC (Aspell et al., 2009; Blanke et al., 2015; Lenggenhager et al., 2007) also impacts memory retrieval (Bréchet et al., 2020, 2019). In two separate behavioral VR experiments, we found improved memory retrieval in conditions when participants had previously seen their own body as part of the virtual scene (online, tracked) during an encoding session performed in immersive 3-dimensional VR scenes. This memory improvement was absent when participants were exposed to identical VR scenes lacking the participant's virtual body, or with a virtual control object instead of the participant's virtual body. Based on these behavioral findings, it was argued that online multisensory integration of visual, somatosensory, and motor inputs impacts the encoding of episodic memories and their later recall (Bréchet et al., 2019). Yet, the neural mechanisms of such BSC-related modulations on EM remain to be investigated and are the subject of the current study.

EM is highly dynamic, and its study is tied to several constraints: the necessity of controlling the encoded material - at the risk of reducing its personal significance - and the risk of interference and re-encoding processes when probing personal life events (Cabeza and St Jacques, 2007). Seminal EM studies used word lists or visuospatial material that are highly controlled but less personally relevant (Thomson and Tulving, 1973). Conversely, refined designs build upon extensive interviews about one's life episodes, thus probing highly personal memories without a reality check and being sensitive to repeated testing (Kopelman et al., 1989). Despite their respective importance in the field, both approaches further lack a perceptual match between encoding and retrieval context, and do not allow to check if the probed memories happened as reported. Several new lines of research have successfully tackled these limitations. Most of them rely on creating or recording real-world stimuli, either by following a controlled scenario such as the exploration of specific real places (Cabeza et al., 2004; St. Jacques and Schacter, 2013), by recording the participant's daily activities (prospective method paradigms - Vogel and Schwabe, 2016), or by using video games designs (Plancher et al., 2013, 2012). These new approaches present the strong asset of being naturalistic, interactive and entertaining while keeping control on the encoded material. The development of computer-based VR technologies provides an elegant alternative to these previous approaches as they allow to precisely control the content of experienced events while enabling interactions during both memory encoding and retrieval. Here, we adapted our immersive VR approach to fMRI in order to investigate the neural mechanisms of EM formation and its modulation by viewing one's body during encoding.

The investigation of the neural substrates of EMs has followed several approaches. The so-called engram - the physical implementation of memories in the brain - is thought to involve functional connections between the neocortical regions processing the perceptual details of experienced events and the hippocampal formation (Moscovitch et al., 2016). In the standard consolidation model of long-term memory (Squire et al., 2015; Squire and Alvarez, 1995), memories are originally dependent on the hippocampus, and become gradually stored in the neocortex over repeated retrievals, with the hippocampus acting as a connection hub to bind disparate neocortical areas. However, theoretical arguments and empirical evidence suggest that EMs remain linked to hippocampal activity for several years when associated with a vivid reliving experience (Moscovitch et al., 2005; Piolino et al., 2004).

In the present study, we used an immersive VR environment enabling one group of participants to encode visual scenes while additionally seeing their own body from first-person perspective and as part of the virtual scene ("body view" group), whereas the other group did not. The "body view" condition thus simulates the ecological co-perception of one's own body (Blanke et al., 2015) during episodic encoding, similarly to Bréchet et al. (2019, 2020). First, we investigated whether EM performance is modulated by first-person body view, delay and the number of objects changed. We used two post-encoding delays, namely a one-hour delay as in Bréchet et al. (2019), and one-day delay after encoding, i.e., after sleep-induced changes in order to capture EM consolidation (Stickgold, 2005). Second, we investigated the impact of first-person body view on ANC measured by a questionnaire one month after the original encoding. Third, in the main part of the current study, we investigated the modulation of functional connectivity measured with fMRI by these factors. Given the constraints and current limitations of immersive VR in the MR magnet, however, we did not investigate brain activity during encoding directly, but recorded immediate pre- and post-encoding - i.e. peri-encoding - resting-state activity. We predicted an increase of memory performance with delay, the number of objects changed and body view as well as an increase of ANC ratings with body view. For recorded brain activity, we predicted a change of the hippocampal and hippocampal-neocortical connectivity between pre- to post-encoding resting-state connectivity (Cohen et al., 2015; Staresina et al., 2013; Stevens et al., 2010; Tambini et al., 2010; Tambini and Davachi, 2019, 2013; van Kesteren et al., 2010) and that this change would differ for participants that saw their body during immersive VR encoding as compared to participants who did not.

2. Materials and methods

2.1. Participants

Thirty right-handed participants (BODY group age 26.3±2.8 years old; 15 participants, 6 males; NOBODY group age 24.4±2.4 years old; 15 participants, 11 males) with normal or corrected-to-normal vision and no history of psychological disorders participated in the study. All participants were compensated for their participation and provided informed written consent in accordance with the Cantonal Ethical Committee of Geneva (CCER) and the declaration of Helsinki (2013).

The sample size was chosen based on two previous similar studies by Bréchet et al. (2019; 2020) where two groups of 16 participants were compared to detect the body view effect with a targeted effect size of 0.6 (Cohen's d), alpha = 0.05, and an actual effect size of 0.57. *A post-hoc* power estimation with alpha = 0.05 for a two-sample t test with a target effect size of 0.6 gave a power of 0.48 for this behavioral body view effect.

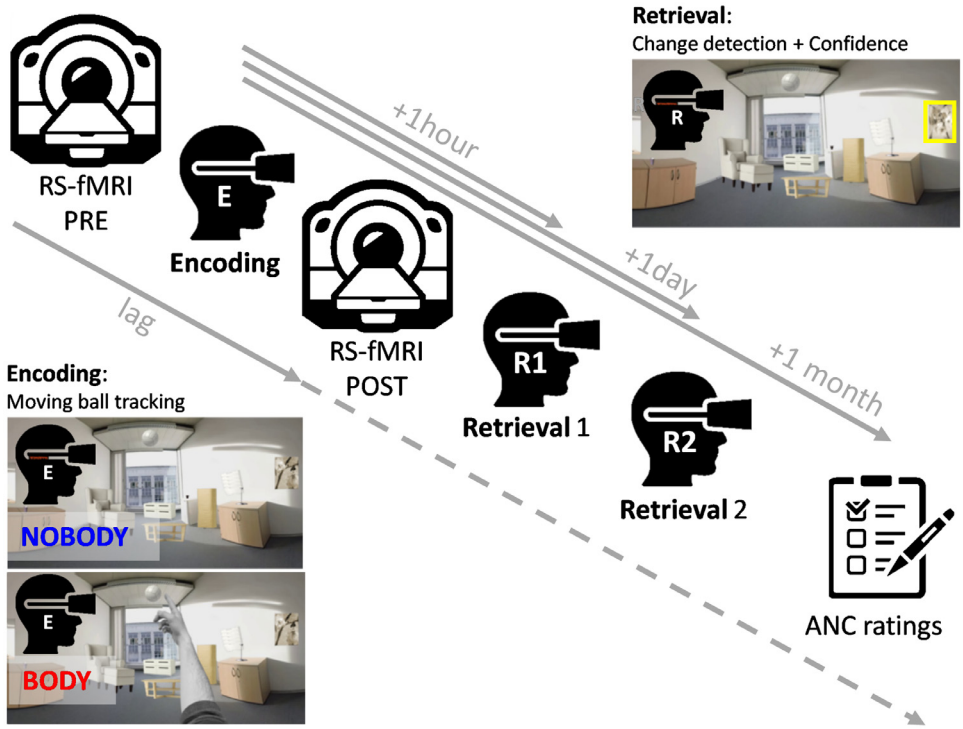

Fig. 1. Experimental design. Both body-viewing (BODY) and body-absent (NOBODY) groups undergo a pre-encoding (RS-fMRI PRE) and a post-encoding (RS-fMRI POST) resting-state functional MRI acquisition. The BODY group encoded visual scenes by performing an incidental moving ball tracking task while seeing their own body in the VR environment (Encoding: BODY). Participants of the NOBODY group did not see their own body during encoding (encoding: NOBODY). Memory retrieval sessions consist of a series of object change detection trials (for instance, the painting highlighted in yellow), each one followed by a confidence judgment, and are performed 1 h and 1 day after encoding (Retrieval 1: +1h, Retrieval 2: +1day). One month after encoding, subjective reliving ratings associated with autonoetic consciousness are rated and reported during the last recall session (ANC ratings).

2.2. Virtual reality (VR) technology

We used the same VR technology as described previously by our team (Bréchet et al., 2019). To summarize, four scenes were recorded from real environments (office rooms) using cameras covering 360 degrees and microphones. They were then reconstructed in virtual reality and displayed trough a head-mounted display (HMD) using a custom software (Realism; see Bréchet et al., 2019;). Using this technology, participants in the BODY group could see their hands, trunk and legs from a first-person perspective and experience the environment as if they were physically present in the scenes.

2.3. Experimental design

Stimuli were identical to the ones we used previously (Bréchet et al., 2019). They consisted of four virtual scenes associated with ten objects each. The objects were extracted from external 2D pictures and added at fixed positions in the scenes. Additionally, ten more objects were associated with each scene for the retrieval testing.

The experiment consisted of three sessions: an incidental encoding period followed by a one-hour delayed retrieval period and a one-day delayed retrieval period. During the two retrieval periods, participants were asked to perform a recognition task. Participants were not informed that they would later be tested on their memory of the stimuli presented during the encoding period. The experimental design is depicted in **Fig. 1**.

2.3.1. Encoding session

During the encoding session, participants had to explore the entire scene and we monitored their attention by asking them to follow a virtual ball moving along a fixed trajectory within each scene for a duration of 2 min. Participants were asked to follow the movements of the ball by pointing at it with their arm outstretched. In total, 4 repetitions of each scene were displayed during the encoding phase.

The main encoding manipulation consisted of showing the participant's physical body (BODY group) or not (NOBODY group) in a between-subject design. Specifically, in the BODY group, the participant's body was inserted in real-time in the virtual scene and displayed so that it appeared as if seen from the natural visual first-person viewpoint. In other words, participants saw their hand, trunk, and legs as if they were part of the virtual scene. In the NOBODY group, the same scenes were displayed, but without the insertion of the tracked body (Fig. 1). The order of presentation of the scenes during encoding was randomized between participants to avoid primacy and recency effects.

2.3.2. Retrieval sessions

The retrieval sessions followed the same procedure as described previously (Bréchet et al, 2019). Participants were exposed to the original or to modified versions of the encoded scenes. Specifically, during a retrieval session, there was no body shown, so that only the encoding manipulation could affect the memory metrics measured during retrieval. Participants performed four blocks of 40 trials. Within each block of 40 trials, we presented 10 trials showing the same environments associated with the same objects as during the encoding session. The remaining 30 trials showed modified scenes where either 1, 2 or 3 new object(s) replaced the original ones shown during the encoding session. The blocks and individual trials within each block were presented in a randomized order. For each trial, participants had to explore the virtual scenes for 10 s and were asked to answer two questions successively. First, participants had to perform a two-alternative forced choice task to indicate whether the virtual scene shown during the retrieval session corresponded to a virtual scene presented during the encoding session. The question was formulated as follows: "Is the scene exactly the same as when you first saw it?". The participants indicated their response with a manual controller paired with the software system. Second, participants were asked to rate how confident they were about their answer via an 11-point rating scale displayed in the HMD (from 0 to 10, corresponding to low and high confidence, respectively). The question was formulated as follows: "How confident were you about your answer?".

We also measured the subjective sense of reliving, or ANC, when the participant recalled the original encoding experience (Fig. 1). This aspect of the retrieval experience is considered difficult to quantify, but several tools have been proposed during cued long-term memory retrieval (i.e., autobiographical interview (Kopelman et al., 1989; Levine

et al., 2002)). There were several constraints: (1) the original encoding was composed of four original scenes and we wished to separate ANC sampling for each of these four scenes, (2) we did not know how classical autobiographical memory questionnaires would conform to a simple and short virtual experience, (3) we wanted a self-report from the participants to minimize experimenter biases. Thus, we used the eight items composing the autonoetic subscale of the Episodic Autobiographical Memory Interview (EAMI (Irish et al., 2008; Irish et al., 2011a)), namely: Viewer Perspective, Mental Time Travel, Vividness, Visual Continuity, Covert Rehearsal, Overt Rehearsal, Overall Re-Experiencing and Emotional Re-Experiencing, and build a questionnaire based on these eight items, asking each participant to rate their subjective experience corresponding to each, for each of the four scenes (**Table S2**). As the retrieval task involved a series of trials exposing the participant to altered versions of the scenes, we provided screenshots of the original scenes emptied from all the objects and presented from different angles (compatible with the experienced first-person perspective) as cues to remember the original exposure to virtual scenes. Thus, ANC was attributed to each encoded scene trying to avoid ambiguity (e.g. confusing one scene with another one or confusing the encoding memories with the retrieval testing memories). We also avoided using the ANC evaluation with the immersive virtual reality as it would have altered the report of the original subjective experience. Finally, dyads of objects/distractors (used in the two retrieval sessions) were presented to the participants, and they were asked to recognize the original objects from the distractors. A one-month delay was determined as a reasonable trade-off for using the autonoetic subscale of the EAMI questionnaire (Irish et al., 2011a) to probe phenomenological characteristics of hippocampal-dependent yet consolidated long-term episodic memories (Dudai, 2012, 2004; McGaugh, 2000; Squire et al., 2015).

2.4. Statistical analysis of behavior

To investigate memory performance, d' and criterion served as synthetic measures of memory performance in a signal-detection theory framework (Green and Swets, 1966): trials were classified as hits (answer: yes, stimulus: yes), false alarms (answer: yes, stimulus: no), misses (answer: no, stimulus: yes) or correct rejections (answer: no, stimulus: no) and then d' were computed as d' = Z(hit rate) − Z(false alarm rate), and criterion as 0.5*(Z(hit rate) + Z(false alarm rate)), where Z is the inverse cumulative distribution of the Gaussian function.

D', criterion, confidence, and reaction time (RT) were analyzed using repeated-measures analyses of variance (ANOVA). The factors introduced in each of the ANOVA were the effect of body view (BODY/NOBODY group) as a between-subject factor, and with the effect of delay (+1 h vs +1 day) and object change (0, 1, 2 or 3 object(s) changed) as within-subject factors. *Post-hoc* testing was done using unpaired t-tests for the body view factor (between-subject) and paired t-tests for the other factors (within-subjects).

To investigate the effect of body view (between-subject) on ANC, questionnaire answers were analyzed with unpaired t-tests, each with Vividness = Vivid, Visual Continuity = VisC, Covert Rehearsal = CR, Overt Rehearsal = OR, Overall Re-Experiencing = ORE and Emotional Re-Experiencing = ERE as dependent variable and logistic generalized linear models with Mental Time Travel = MTT and Viewer Perspective = ViewerP as dependent variables. All models took group as an independent variable. As a further exploration of the results showed a high inter-subject correlation for these ratings, a dimensionality reduction was performed using principal component analysis with the FactoMineR (https://cran.r-project.org/web/packages/FactoMineR/index.html) and factoextra (https://cran.r-project.org/web/packages/factoextra/index.html) R packages, as described later in the results. Principal components were selected based on the Scree plots and on explanatory power (percentage of variance) with respect to the original variables.

Finally, the relation between ANC and memory performance was analyzed using linear modelling. The factors introduced in the model were the effect of body view and d'. Two models were computed: one for the +1 h delay and a second for the +1 day delay.

All statistical tests included the gender of the participants as a covariate (between-subject), as gender has been shown to impact memory metrics (Yagi and Galea, 2019) and the groups were not balanced for this variable.

2.5. MRI acquisition

MR images were acquired using a 3T MRI scanner (MAGNETOM PRISMA; Siemens) using a 32-channel head coil at Campus Biotech Geneva (https://www.campusbiotech.ch/). Each participant underwent 5.21 min anatomical imaging using a T1-weighted MPRAGE sequence (192 slices; slice thickness = 0.90 mm; repetition time = 2300 ms; echo time = 2.32 ms; flip angle = 8°; voxel size= $0.9 \times 0.9 \times 0.9$ mm^3; FOV = 240 mm; GRAPPA factor = 2). They also underwent pre- and post-encoding 12-min sessions of resting-state functional imaging with blood oxygenation level-dependent contrast using a gradient-echo echo-planar imaging sequence (46 slices; slice thickness = 2.5 mm; repetition time = 2000 ms; echo time = 30 ms; voxel size = $2.5 \times 2.5 \times 2.5$ mm^3; FOV = 200 mm; GRAPPA factor = 2).

2.6. Resting-state functional connectivity analysis

2.6.1. Rationale

In the present study, we used fMRI to record peri-encoding activity; i.e., the brain activity that occurs immediately prior to the onset and following the offset of the content to be remembered (Cohen et al., 2015). Notably, post-encoding resting-state connectivity has proven efficient in predicting EM outcomes (Stevens et al., 2010; Tambini et al., 2010; Tambini and Davachi, 2013; van Kesteren et al., 2010), as it arguably reflects the initiation of memory consolidation. Here, we adopted a classical pre/post encoding resting-state acquisition and targeted both medial temporal and relevant neocortical areas.

Our imaging analysis followed 3 successive steps. First, functional connectivity analysis was performed using a Region of Interest (ROI)-to-ROI analysis for the *a priori* network of interest and selected the seeds responsive to body view, lag and their interaction. Second, we extracted the connectivity patterns between those relevant seeds and the whole brain that showed body view and lag effects. Third, we directly investigated the connections showing significant correlations with ANC in conjunction with body view and lag effects.

Bivariate correlation is used as a functional connectivity measure between two areas. The CONN implementation of a general linear model (GLM) was used for comparison of connectivity results within group (PRE vs POST) as well as between groups (BODY vs NOBODY).

2.6.2. MRI preprocessing

Resting-state fMRI data were preprocessed using SPM12 v6906 and analyzed using the CONN toolbox v18a (www.nitrc.org/projects/conn). Each subject's functional volume underwent slice timing, was realigned to the first volume, was co-registered with the anatomical image and was normalized to the Montreal Neurological Institute template. Resulting functional images were smoothed with a 5 mm full width at half maximum Gaussian kernel. The structural MRI scans were segmented to provide grey matter, white matter and cerebrospinal fluid maps using default tissue probability maps as priors. Time-courses from the components associated with white matter and cerebrospinal fluid (CSF) produced during the segmentation step were regressed out of whole-brain gray matter activity. Twelve motion regressors (estimated subject motion parameters and their derivatives over time) were used to control for correlations during movement. Cardiac pulse and respiration artifacts were recorded with a photoplethysmograph and a respiration

belt (BIOPAC MP150) and resampled with respect to the MRI pulse timing. Cardiac pulse, respiration and motion were regressed out of the signal. Data were band-pass filtered between 0.008 and 0.09 Hz; session-specific linear detrending was performed. Regression, filtering and detrending were done at the same time using the default preprocessing step of the CONN Toolbox.

2.6.3. ROI-to-ROI connectivity

In order to investigate whether resting-state functional connectivity was modulated differently by encoding 3D scenes while viewing one's own body or not and how this changed depending on delay, we conducted an ROI-to-ROI analysis in an *a priori* network. We selected a set of regions known for their predictive power on memory performance: the bilateral hippocampus, bilateral parahippocampus, and bilateral medial prefrontal cortex (mPFC - van Kesteren et al., 2010). We also selected the main regions involved in BSC: the bilateral temporal-parietal cortex (see Ionta et al., 2011) and bilateral posterior insula (Tsakiris et al., 2006; for review see Grivaz et al., 2017). We investigated both *a priori* networks to target hypothesis-driven mechanisms, and also conducted follow-up exploratory seed-to-voxel analyses to extend our understanding of the underlying neural mechanisms.

We built those *a priori* regions of interest from the Brainnetome atlas (Fan et al., 2016; http://atlas.brainnetome.org/): the bilateral hippocampus was obtained by the fusion of rostral and caudal hippocampal subparts, the bilateral parahippocampus was obtained by the fusion of 6 sub-regions (A35/36r, A35/36c, TL, TI, A28/34 and TH), the bilateral medial part of the orbital gyrus (A14m) was taken as medial prefrontal cortex, and the bilateral posterior insula was obtained by fusion of 3 regions: hypergranular insula, vId/vIg and dlg. Bilateral temporo-parietal junctions were created as 3 mm-wide spheres centered on coordinates found in Ionta et al (2011). In total, 10 regions were entered in an *a priori* ROI-to-ROI analysis.

Connectivity values (Fisher z-transformed correlation coefficients) between each dyad of ROI were extracted from the connectivity map and passed onto a second-level mixed GLM. At the second level for each contrast, we selected only the connections surviving an FDR-correction for the total number of bilateral connections (p = 0.05, FDR-corrected for 45 connections). On the second-level, we performed paired two-sample t-tests between BODY and NOBODY groups (body view effect), paired two-sample t-tests between PRE- and POST-encoding sessions (lag effect) and unpaired two-sample t-tests for body view-by-lag Interaction, all using the CONN toolbox interface. ROI-to-ROI connectivity was represented using plotting utilities from nilearn, a python-based toolbox for brain imaging; https://nilearn.github.io/index.html).

2.6.4. Seed-to-whole brain connectivity

We selected a subset of the *a priori* regions of interest based on the results of the ROI-to-ROI investigation. Then, we submitted each ROI of this subset to a seed-to-whole brain connectivity analysis: body view, lag, body view-by-lag effects were investigated using a similar GLM as for ROI-to-ROI analyses. We combined these 3 effects in a covariate analysis with the first PCA component that we obtained from the subjective ratings analysis, which identify to ANC, investigating the neural correlates of subjective experience at retrieval and their modulation by our conditions of interest.

To threshold the brain maps, we used a cluster-level inference based on permutation analyses (Bullmore et al., 1999) as implemented in CONN. Instead of relying on the classical Random Field Theory (RFT) assumptions about the cluster probability distribution, it estimates the probability density function of each cluster size under the null hypothesis, using 1000 permutation of the original data to simulate this null hypothesis. Second, nonparametric analyses rely on each cluster mass (i.e., the sum of the T-squared or F- statistics across all voxels within each cluster), instead of cluster size. As compared to parametric methods, non-parametric methods reduce the inflated false positive rates using cluster-level inference (Thirion et al, 2007; Eklund et al, 2016), especially for modest samples. For nonparametric analyses reported in the main text and as the main result, we used a cluster-forming threshold of $p < 0.001$ (uncorrected) and an FDR-corrected cluster-mass threshold of $p < 0.05$ (two-tailed t-tests).

We also performed parametric RFT-based analyses in order to provide a picture of the underlying subthreshold patterns. We used a cluster-forming threshold of $p < 0.001$ and an FDR-corrected cluster threshold of $p < 0.05$ (two-tailed t-tests). The corresponding results are provided as supplementary material (**Tables S1**, **S3** and **S4** and **Fig. S4**, and **Fig. S5**).

All ROI-to-ROI and seed-to-whole brain statistical tests included the gender of the participants as a covariate of non-interest (between-subject), as it has been shown to impact memory metrics (Yagi and Galea, 2019) and the groups were not balanced for this variable.

3. Results

3.1. Behavioral results

We investigated memory performance, memory confidence and reactions times (RT) and tested the effects of the body view, the delay between encoding and retrieval, as well as the number of objects changed between the encoding and retrieval trials (**Fig. S1**). We also investigated the effect of the body view on ANC using with ratings adapted from the EAMI (Irish et al., 2008; Irish et al., 2011b) that were probed during a memory recall one month after encoding the original scenes.

3.1.1. Memory performance

An ANOVA on memory performance showed that d' increased with the delay ($F(1, 26) = 7.62$, $p = 0.01$, partial $\eta^2 = 0.068$) and with the number of object changes ($F(2,52) = 44$, $p < 0.001$, partial $\eta^2 = 0.085$). However, d' did not significantly vary between the BODY and NOBODY groups $F(1,26) = 0.45$, $p = 0.51$, partial $\eta^2 = 0.011$, BF_10 = 0.66). We found a triple gender*delay*number of object changed interaction ($F(2,52) = 3.37$, $p = 0.042$, partial $\eta^2 = 0.003$), and post-hoc analyses revealed a higher increase of d' with delay when the number of object changed = 3 in male than female participants ($t(30) = 2.25$, $p = 0.032$). The criterion decreased significantly with the number of objects changed ($F(2,52) = 44$, $p < 0.001$, partial $\eta^2 = 0.11$), reflecting more correct rejections. We found for criterion a triple gender*delay*number of object changed interaction ($F(2,52) = 3.37$, $p = 0.042$, partial $\eta^2 = 0.004$), but post-hoc analyses revealed no significant difference (6 t-tests, delay effect tested across number of object changed levels and gender groups). Finally, RT significantly decreased with delay ($F(1,26) = 21.1$, $p < 0.001$, partial $\eta^2 = 0.14$) and with the number of object changes ($F(2,52) = 26.6$, $p < 0.001$, partial $\eta^2 = 0.03$). This shows that memory performance and decision time increased over time and with more distractors.

ANOVAs were also conducted on memory confidence. As predicted, confidence increased with the number of object changes ($F(2,52) = 36.6$, $p < 0.001$, partial $\eta^2 = 0.022$). No other factors or interactions were significant. Reaction times for confidence judgments were significantly reduced with delay ($F(1,26) = 27.4$, $p < 0.001$, partial $\eta^2 = 0.2$) and with the number of object changes ($F(2,52) = 40.8$, $p < 0.001$, partial $\eta^2 = 0.04$). A significant 3-way interaction was observed (delay*body view*number of object changes ($F(2,52) = 4.1$, $p = 0.022$, partial $\eta^2 = 0.0028$). However, no significant difference was found with *post-hoc* analysis. This shows that confidence followed memory performance, increasing with the discrepancy between original and test scenes.

3.1.2. Autonoetic consciousness ratings

First, the exploration of ANC ratings revealed that the different items were highly inter-correlated (Fig. S2A). We performed Principal Component Analysis (PCA) to extract the main components and focused further analyses on the main components of ANC. PCA revealed three main components based on the scree-plot break criterion (Cattell, 1966) (Fig.

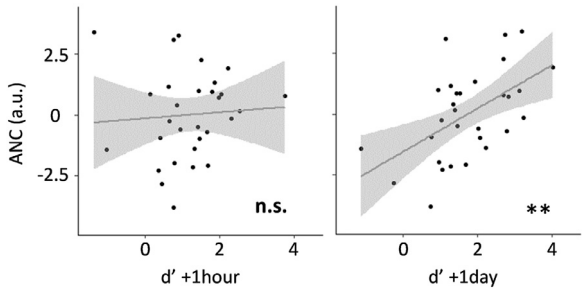

Fig. 2. Autonoetic consciousness (ANC) is positively correlated to delayed memory (d'+1day). Subjective reliving ratings associated with ANC were significantly correlated to memory performance measured one-day (d'+1day) but not 1 h (d'+1h) after encoding, suggesting that ANC formation is related to sleep-related memory consolidation. ** $p < 0.01$; n.s. not significant.

S2B). PC1, PC2 and PC3 accounted respectively for 41%, 16.7% and 11.7% of total variance. The first principal component (PC1) was positively weighted for all the metrics and likely represents the global intensity of ANC at retrieval (**Fig. S2C**). The second component (PC2) was negatively weighted for MTT, ORE, ViewerP, and Vivid, but positively weighted for VisC, CR, OR, and ERE. The third component (PC3) was more heterogeneous, positively correlating with ViewerP, OR, and CR, and negatively with Vivid, VisC, and ORE. As PC1 accounts for most of the variance and is consistently weighted positively, we considered it as a synthetic metric of ANC and PC1 will represent ANC for all further analyses.

Second, we investigated whether any differences in ANC ratings were caused by body view during encoding (**Table S2**). The effect of gender was also modelled, as gender effects have been reported in the original report of EAMI (Irish et al, 2008). However, no significant effects were found surviving a Bonferroni multiple comparisons correction nor a False Discovery Rate (FDR)-correction (Benjamini- Hochberg procedure). We also checked if the different scenes were differing in term of ANC but did not find any significant results. Bayes factor were calculated and reported for scene effect and indicate either evidence in favor of the null hypothesis (BF_10 < 1/3) or inconclusive evidence for all individual ratings (1/3 < BF_10 < 3). Finally, we explored the relation between ANC and memory performance: we found that ANC was correlated to d'+1 day ($F(1,26) = 10.9$, $p = 0.0028$) but not to d'+1h ($F(1,26) = 0.13$, $p = 0.72$) (Fig. 2). Moreover, ANC was significantly correlated to the d' difference across delays (Δd', $F(1,26) = 8.1$, $p = 0.009$).

3.2. fMRI results

We predicted connectivity changes with respect to body view during the post-encoding (lag = POST) phase as compared to the pre-encoding phase (lag = PRE), i.e., a body view-by-lag interaction, and explored main effects of body view and lag (PRE vs POST) as well.

3.2.1. ROI-to-ROI connectivity in the a priori network

Investigating the connectivity changes between the BODY and the NOBODY group, irrespective of the pre- and post-encoding period (i.e., the main effect of body view), we found significantly higher functional connectivity between rHC and rPHC ($F(2,27) = 9.7$, $p < 0.001$, FDR-corrected $p = 0.028$) and between left and right TPJ ($F(2,27) = 8.7$, $p = 0.0013$, FDR-corrected $p = 0.028$ when participants saw their body during encoding versus when they did not (**Fig. S3A**). We also investigated the functional connectivity changes between the pre- and post-encoding periods, irrespective of the body view factor, (i.e., the main lag effect). However, no significant changes in connectivity survived an FDR-corrected $p < 0.05$ threshold (**Fig. S3B**). The body view-by-lag interaction was significant for the functional connectivity between rHC and rPHC ($T(28) = 3.4$, $p < 0.001$, FDR-corrected $p = 0.042$; Fig. 3**A**). This interaction for the connectivity between lHC and rHC was in the same direction but not significant ($T(28) = 3.03$, $p = 0.0027$, FDR-corrected $p = 0.06$). *Post-hoc* analysis on rHC-rPHC connectivity revealed significantly higher connectivity for the BODY group as compared to the NOBODY group for the post-encoding data (POST: $F(1,28) = 18.7$, $p < 0.001$) and no such effect in the pre-encoding acquisition (PRE: $F(1,28) = 0.002$, $p = 0.96$, **Fig. 3B)**. The effect size of this interaction can be considered large (Cohen's $d = 1.6$). To summarize, these results show that viewing one's tracked body during encoding changes the intrinsic connectivity of medial temporal lobe structures and is associated with an increased connectivity in the post-encoding phase depending on whether the body was seen during encoding. Based on these results, we considered the rHC and rPHC as an EM sub-network of interest for in-depth follow-up analyses.

3.2.2. Seed-to-whole brain connectivity with EM sub-network

To investigate the role of the sub-network consisting of the rHC and rPHC in more details, we next conducted a seed-to-whole brain analysis that consists of quantifying the connectivity between a given seed and each voxel of the brain (Whitfield-Gabrieli and Nieto-Castanon, 2012). Using the rHC, and rPHC as seed regions, we quantified connectivity separately for the main effect of body view (BODY vs NOBODY), the main effect of lag (PPOST vs PRE) and the body view-by-lag interaction. We found no significant effects of body view, lag or body view-by-lag interaction.

3.2.3. Seed-to-whole brain connectivity as correlate of ANC

We also performed an exploratory analysis of seed-to-whole brain connectivity to investigate if the connections between our preselected 2 seeds (rHC and rPHC) and the whole brain are significant correlates of ANC as reported 1 month after the encoding session.

Main effect of Body View and Lag on Correlations Between Connectivity and ANC: Using nonparametric analyses, no significant effects are found.

Interaction Between Body View and Lag on Correlations Between Connectivity and ANC: The results of the seed-to-whole brain interaction for the rHC and rPHC seeds are displayed in Fig. 4, Tables 1 and 2. Investigating the body view-by-lag interaction on rHC and rPHC connectivity with the whole brain, we found that the connectivity between rPHC and Pre/PostC, SMA and SPL displays positive interactions, while the connectivity between rPHC and bilateral precunei (PCun) and cingulate cortex (Cing) displays negative interactions. Decomposing the positive interaction for the Pre/PostC, we found that it is driven by two components: the reversal of a significant negative correlation to significant positive correlation with ANC, between PRE and POST lag, in BODY group, and the emergence of a significant negative correlation with ANC in the POST lag, for the NOBODY group. Decomposing the positive interaction for the SMA, we found that it is driven by two components: the emergence of a significant positive correlation with ANC in lag POST in BODY group and the emergence of a significant negative correlation with ANC in lag POST for the NOBODY group. Decomposing the positive interaction for the SPL, we found that it is driven mainly by the emergence of a significant positive correlation with ANC in lag POST in BODY group. Decomposing the negative interaction for the Cing, we found that it is driven by two components: a reversal of significant positive correlation to significant negative correlation with ANC between PRE and POST lag in BODY group and the removal of a significant negative correlation with ANC at lag PRE for the NOBODY group. Decomposing the negative interaction for the PCun, we found that it is driven mainly by the removal of pre-encoding correlation, respectively negative and positive for the NOBODY and BODY groups.

Additional analysis on individual ANC questionnaire items performed to investigate if the PCA reduction altered the pattern of connectivity related with ANC confirmed the results obtained with PC1 and revealed very similar antagonistic networks (**Fig. S6; Table S5).**

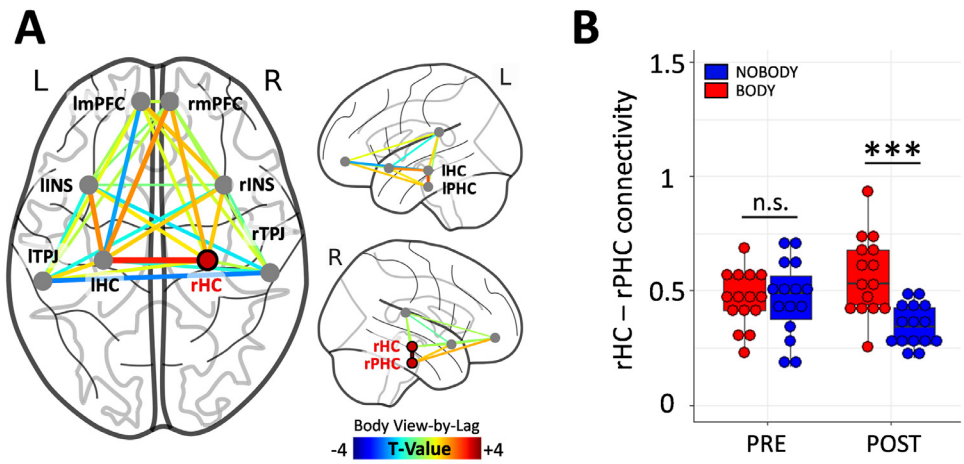

Fig. 3. Body view-by-lag effect in the *a priori* network. A. Glass-brain view of the seeds and connections tested in the ROI-to-ROI analysis: bilateral hippocampi (lHC and rHC), bilateral parahippocampi (lPHC and rPHC), bilateral medial prefrontal cortex (lmPFC and rmPFC), bilateral posterior insula (lINS and rINS), bilateral temporo-parietal junction (lTPJ and rTPJ). The color of the connection reflects the T-value calculated for the body view-by-lag interaction. Significant connections are highlighted with a bold black outline and the names of the corresponding nodes are displayed in red. B. Mean connectivity values across lag (PRE and POST) and body view (BODY and NOBODY groups) for the connection that exhibit significant Body-View-by-lag interaction and *post-hoc* significant increased connectivity for lag POST between BODY and NOBODY group. Post-hoc significance: *** $p < 0.001$; n.s. non-significant.

Table 1
Seed-to-whole brain connections showing significant correlations with ANC, modulated by lag and body view. rPHC: right parahippocampus; Pre/PostC: Precentral and postcentral gyrus; SPL: Superior parietal lobule; SMA: Supplementary motor area; Cing: Cingulate cortex; PCun: Precuneus; df: degree of freedom; Tmin: minimum T-value; K: cluster extent; L: left; R: right; pos: positive; neg: negative.

	df	Tmin	K	MNI coordinates			Seed	Laterality	Cluster Label	sign	cluster.mass FDR p
ANC*lag*body view	25	3.73	635	-4	-32	62	rPHC	L+R	Pre/PostC	pos	0.017
	25	3.73	86	-30	-54	66	rPHC	L	SPL	pos	0.037
	25	3.73	68	-10	-8	60	rPHC	L+R	SMA	pos	0.045
	25	3.73	175	4	-30	26	rPHC	L+R	Cing	neg	0.017
	25	3.73	169	-12	-66	36	rPHC	L	PCun	neg	0.017
	25	3.73	122	16	-72	36	rPHC	R	Pcun	neg	0.024

Table 2
Exploration of seed-to-whole brain interactions and description of main patterns. For each connection showing a significant ANC*lag*body view interaction, the interaction is described by the sign and the post-hoc correlation coefficients between connectivity and ANC; i.e., if connectivity correlates with ANC for PRE and POST and for BODY or NOBODY group. Two main patterns emerge from this exploration. First, positive interactions are mostly driven by positive correlations with ANC for the BODY group at lag POST (cf. "POST corr." and "PRE/POST reversal" for positive interactions in Table 1), i.e., after encoding 3D virtual scenes with body view enabled. Second, negative interactions are mostly driven by the disappearance of negative correlations for the NOBODY group and positive correlations for the lag PRE (cf. "PRE removal" for negative interactions in Table 1), i.e., correlation with ANC pre-existing to 3D scenes encoding. SMA: Supplementary Motor Area; Pre/PostC: Precentral and Postcentral cortex; SPL: Superior Parietal Lobule; Cing: Cingulate Cortex; pos: positive; neg: negative. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

		Conditions: Linear regression coefficient				Pattern driving interaction	
Connection	Sign	ANC: NB PRE	ANC: B PRE	ANC: NB POST	ANC: B POST	NOBODY	BODY
rPHC-Pre/PostC	pos	0.46	**-0.76****	**-0.66****	**0.63****	**POST corr**	**PRE/POST Reversal**
rPHC-SMA	pos	0.28	-0.22	**-0.61***	**0.66****	**POST corr**	**POST corr**
rPHC-SPL	pos	0.51	0.14	-0.51	**0.64****	trend reversal	**POST corr**
rPHC-Cing	neg	**-0.78*****	**0.81*****	-0.06	**-0.64***	**PRE removal**	**PRE/POST Reversal**
rPHC-lPcun	neg	**-0.52***	**0.61***	0.22	-0.32	**PRE removal**	**PRE removal**
rPHC-rPcun	neg	-0.49	**0.72****	0.07	-0.34	trend reversal	**PRE removal**

4. Discussion

We report several novel findings on EM and ANC, and in particular about potential neural mechanisms of memory encoding subsequent to the perception of one's own body during the encoding of scenes in immersive VR, as measured by peri-encoding resting-state connectivity.". First, we found delay- and context-dependent memory performance - typically observed in EM research - and related it to ANC measured after long-term consolidation, showing that our VR setup provides controlled immersive 3D scenes susceptible to become genuine EM. Second, we found that the connectivity within the right medial temporal lobe changed with body view: functional connectivity between the rHC and rPHC was increased when participants saw their body and was decreased when the body was absent during encoding. Finally, the connectivity between the medial temporal lobe and the neocortex, including notably the primary somatosensory and motor cortices - was correlated with ANC, depending on whether participants saw their body during encoding or not. This suggests that subjective reliving associated with ANC may capitalizes on sensorimotor mechanisms that have been linked to bodily self-consciousness. This is the first evidence of a modulation of the EM networks activity by the incidental co-perception of one's own body, extending previous behavioral evidence using the same VR platform (Bréchet et al., 2019, 2020).

4.1. Delay- and context-dependent memory of virtual scenes

As developed previously in behavioral research (Bréchet et al., 2019, 2020), the present VR setup provides a precise control of encoding conditions while being highly naturalistic and allowing to reproduce sensorimotor contingencies (Slater and Sanchez-Vives, 2016). Using this im-

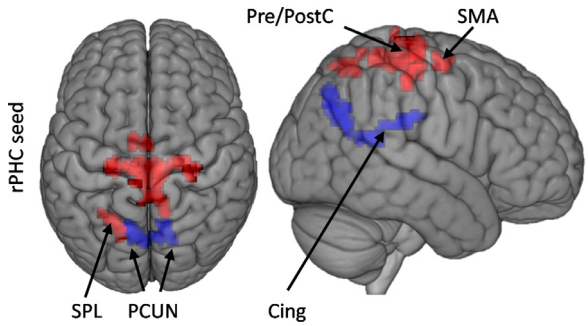

Fig. 4. Seed-to-whole brain connectivity antagonistic patterns characterize the correlates of autonoetic consciousness in BODY and NOBODY groups and between lag Pre and Post. The connectivity between the rPHC and the displayed regions is correlated with autonoetic consciousness (ANC) and modulated by body view and lag. The decomposition of each interaction is displayed in Table 2. rPHC: right ParaHippocampus; SPL: Superior Parietal Lobule; PCUN: Precuneus; Cing: Cingulate cortex; PreC: Precentral cortex; PostC: Postcentral Cortex; SMA: Supplementary Motor Area. Blue color: negative interaction, red color: positive interaction.

mersive VR setup, we investigated memory retrieval of encoded scenes and replicated some of our previous behavioral findings.

First, memory performance for the original scenes improved after a one-day delay as compared to a one-hour delay. This is consistent with the standard model of consolidation of memories over sleep (Stickgold, 2005) that have been found in both animal and human EM (Aly and Moscovitch, 2010). This is also suggesting that the memory engram dynamically changed between one-hour and one-day delays (Dudai, 2012). Second, we replicated previous observations of improved memory performance with the discrepancy between original scenes and lures (Bréchet et al., 2019). This effect was notably not affected by the delay, suggesting that the initial memory encoding already allowed participants to detect subtle changes in their composition when exposed to lures. Thus, the present behavioral findings show that dynamical neural changes were triggered by the initial exposure to the scenes that led to later improvements of early EM performance. This is suggesting that post-encoding brain activity may capture dynamical change relevant for memory encoding and consolidation.

In the present fMRI investigation, we replicated the behavioral effects of delay and number of object changes on memory performance, but did not confirm improved memory performance depending on body view one hour after encoding, as reported in two behavioral studies (Bréchet et al., 2019, 2020). Several differences between these studies may account for this. First, as wakeful rest following immediate encoding is known to improve memory (Dewar et al., 2014; Martini et al., 2018; Mercer, 2015), it remains possible that the scanning process may have interfered with the ongoing memory formation. Second, the experimental protocols differed. Finally, the calculated Bayes factor suggests that the absence of effect is inconclusive (i.e. absence of evidence in either direction) for our modest sample of participant.

4.2. Consolidated memory is associated with autonoetic consciousness

ANC has been proposed to be an important subjective component of remembering since its original formulation by Endel Tulving (Baddeley, 2001; Brewer and Pani, 1996; Gardiner, 2001; Tulving, 2001). Former studies used the remember/know (R/K) paradigm where participants are asked to classify their recognition as acts of remembering or knowing (Tulving, 1985), remembering being associated with ANC. Yet over the years, the R/K dichotomy has been more related to memory strength than ANC (Squire et al., 2007). In the present study, we modified the autonoetic subscale of the episodic autobiographical memory interview (EAMI; Irish et al., 2011a, 2008) to assess components of the subjective re-living experience associated with ANC, as directly reported by the subject. We found a relation between 1 day-delayed memory performance and ANC: the better the memory performance, the stronger was the overall subjective experience of reliving. Low performance and weak experience of reliving have been associated together with age (Piolino et al., 2006) or memory impairments in Alzheimer's disease (El Haj et al., 2016, 2015). Here we complete this view by showing a positive relation between the objective and subjective components of memory recall. As our task consist in the correct identification of spatial scenes, this is also in line with the recent idea that the subjective experience in EM retrieval is intimately bound to spatial scene representation (Rubin and Umanath, 2015), and as postulated by the scene construction theory of EM (Hassabis and Maguire, 2007, 2009). As we found this relation only with 1-day delayed memory, we suggest that only consolidated memory is related to ANC. We did not find any effect of body view on ANC measures, suggesting that the manipulation of body view at encoding did not led to a noticeable difference of subjective reliving by the participants. Further research should investigate more subtle measures of bodily self-consciousness during encoding to uncover the role of first-person body view on ANC.

4.3. Body view increases the connectivity within the right temporal lobe

One's own body perception trough multisensory signals (visual, somatosensory, vestibular, and motor signals) has been linked to self-related processing and notably BSC (Blanke, 2012; Blanke et al., 2015; Blanke and Metzinger, 2009). Recent work further showed that modulations of BSC, like first-person perspective, also impact EM encoding. Notably, Bergouignan et al. (2014) reported that recall of items and hippocampal activity during the encoding of episodic events is modulated by the visual perspective from where the event was viewed during encoding: the authors reported better EM for first-person versus third-person perspective encoding. Recent evidence is also compatible with the proposal that visual body perspective may affect EM retrieval via a distinct connectivity pattern originating from medial temporal regions and directed to the neocortex (Iriye and St. Jacques, 2018).

Here, we observed enhanced connectivity within the right medial temporal lobe between the pre- and post-encoding periods, in the group of participants that saw their body during encoding. Moreover, the opposite trend was observed when the body was absent during encoding, while all other aspects of testing during encoding and all aspects in the pre- and post-encoding experience were identical. This increase of within-temporal lobe connectivity may reflect EM encoding-related neural changes. In the EM literature, the encoding and recollection of events have been related to hippocampal activity in human neuroimaging studies (Yonelinas, 2001) and in human lesion studies (i.e., Scoville and Milner, 1957). Intrinsic medial temporal connectivity has been correlated to individual memory performance in EM (Wang et al., 2010) and parahippocampal-hippocampal connectivity is specifically increased for episodic autobiographical memory as compared to nonpersonal long-term memories (Maguire et al., 2000). Finally, effective connectivity between left and right hippocampi was found during distinct phases of autobiographical memory retrieval (McCormick et al., 2013). Regarding the existing literature, our findings suggest that first-person body view - by modulating intrinsic medial temporal connectivity – may impact the encoding and later recall of episodic autobiographical memories (Ritchey et al., 2012; Rugg, 2002).

4.4. Body view modulates the neural correlates of autonoetic consciousness

We found two distinct networks whose activity levels correlated with ANC ratings and showed fluctuations with respect to our experimental manipulation (pre- vs post-encoding) that differed between participants that encoded the scenes with a body view or not. The first network was composed of fronto-parietal regions. In this network, the connectivity between the rPHC and fronto-parietal regions correlated with ANC after the encoding manipulation, but only in the group that encoded scenes

with first-person body view. Thus, the incidental exploration of virtual 3D scenes triggered a connectivity modulation between the medial temporal cortex and this second network that predicts later ANC during retrieval. Of note, bilateral SPL and S1 have all been related to multisensory bodily processing, including BSC (for reviews, see Blanke et al., 2015; Grivaz et al., 2017). The post-encoding correlation between ANC and the functional connectivity between the medial temporal lobe and multisensory regions of the fronto-parietal cortex, in the Body view condition, may supports our proposal that multisensory processing related to body view have been integrated with the engram. Alternatively, these regions have been related to many other cognitive functions, like visuospatial processing or reaching, that could account for the observed activity.

The second network displayed a negative ANC-by-lag-by-body view interaction and was prominently composed of connections between the right hippocampus and parahippocampus and the bilateral medial precuneus and cingulate cortex. In this network, the interaction was largely driven by the disappearance of pre-encoding correlations with ANC after our experimental manipulation. The precuneus is part of the core default-mode network (Mazoyer et al., 2001; Raichle et al., 2001) and has been related to self-consciousness (Cavanna and Trimble, 2006), but also EM (Sheldon et al., 2016). Specifically, the precuneus is activated in response to viewpoint change in space, time and person (Gauthier and van Wassenhove, 2016; Peer et al., 2015) but also in perspective taking in autobiographical memory (St. Jacques et al., 2016; St. Jacques, 2019). Here, we found that pre-existing correlations between ANC scores and the connectivity between medial temporal areas and this network are disrupted after viewing virtual 3D scenes. We suggest that both networks may be part of a system related to BSC that functions through antagonistic up-down regulation. Future studies should investigate not only body view effects but also other factors of BSC during encoding (associated with changes in body ownership, self-location and first-person perspective), and relate these experimentally altered states of BSC with later changes in ANC and EM performance. Overall, we found two antagonistic large-scale networks defined by their connectivity with the medial temporal cortex and their relationship to ANC. While the first one, related to post-encoding modifications by body view, comprises a set of regions related to multisensory bodily processing, peripersonal space coding, and BSC, the second one related to pre-encoding activity and visual input. This suggests that distinct aspects of BSC may be differentially involved in the building of ANC, with potentially antagonistic relations.

It would have been interesting to test other classical effects of BSC and their potential impacts on episodic memory. Thus, optimal multisensory integration associated with BSC requires that somatosensory or motor information to be linked with a visual cue in the shape of a body. For instance, displaying a visual control object instead of the image of a human body leads to no or to weaker multisensory integration and modulation of BSC (i.e. Blanke et al, 2015). This effect has been reported for episodic memory in a previous experiment (Bréchet et al., 2019). Moreover, in the present study, the participant's seen outstretched arm was actively involved in the exploration of the virtual scene and the related motor signals may additionally modulate BSC (and memory). Future work should control such additional sensorimotor mechanisms by comparing conditions where the body would be moved passively or by inserting spatio-temporal conflicts between the seen movement and the participant's movements (embodiment factor; i.e. Blanke et al., 2015). Additional measurements of self-identification, body ownership, and the sense of agency could be acquired as well. Due to the already heavy time constraints of the present study and procedure, lasting a total of 3 h on three separate days and distributed over 1 month, we were not able to test these additional conditions and their potential impacts on episodic memory in the present study.

4.5. Conclusion

The present study highlights the impact of the bodily self on the encoding of episodic memories. The virtual simulation of lifelike 3D scenes gives rises to psychological and neural processes identifiable to episodic autobiographical memory. We provide evidence of a modulation of brain activity related to the encoding and consolidation of episodic autobiographical memories but also to the neural networks involved in the building of autonoetic consciousness. One limitation of the current work is the focus on peri-encoding brain activity. Future works will need to directly tackle the neural correlates of episodic memory encoding *per se*, using an integrated immersive virtual environment combined with MRI.

Declaration of Competing Interest

The authors declare no conflict of interest.

CRediT authorship contribution statement

Baptiste Gauthier: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Lucie Bréchet:** Conceptualization, Methodology, Writing - review & editing. **Florian Lance:** Methodology, Software. **Robin Mange:** Software. **Bruno Herbelin:** Software. **Nathan Faivre:** Formal analysis, Writing - review & editing. **Thomas A.W. Bolton:** Conceptualization, Writing - review & editing. **Dimitri Van De Ville:** Conceptualization, Writing - review & editing. **Olaf Blanke:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Acknowledgments

We thank Dr. Jevita Potheegadoo for fruitful discussions on the first version of the manuscript.

Funding sources

This work was supported by the Bertarelli Foundation, the Human Neuroscience Platform, Fondation Campus Biotech Geneva (FCBG), Geneva, Switzerland, the University of Geneva (UniGe), the Hôpitaux Universitaires de Genève (HUG) and by the Institute of Translational Molecular Imaging (ITMI), and by JST ERATO Grant Number JPMJER1801, Japan.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2020.117370.

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