

**Simulating the situated-self drives hippocampo-cortical engagement  
during inner narration of events**

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*Cerebral Cortex*, bhac047,

<https://doi.org/10.1093/cercor/bhac047>

Published:12 March 2022

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## Abstract

We often use inner narration when thinking about past and future events. The present paradigm explicitly addresses the influence of the language used in inner narration on the hippocampus-dependent event construction process. We assessed the language context effect during the inner narration of different event types: past, future, daydream, and self-unrelated fictitious events. The language context was assessed via a fluent bilingual population who used inner narration, either in their first language (L1) or second language (L2). Not all inner narration of events elicited hippocampo-cortical activity. In fact, only the angular gyrus and precuneus-retrosplenial cortex were activated by inner narration across all event types. More precisely, only inner narration of events which entailed the simulation of bodily self-location in space (whether or not they were time-marked: past, future, daydream) depended on the hippocampo-cortical system, while inner narration of events that did not entail bodily self-location (self-unrelated fictitious) did not. The language context of the narration influenced the bilinguals' hippocampo-cortical system by enhancing the co-activation of semantic areas with the hippocampus for inner narration of events in the L2. Overall, this study highlights 2 important characteristics of hippocampo-cortical-dependent inner narration of events: The core episodic hippocampal system is activated for inner narration of events simulating self-location in space (regardless of time-marking), and the inner language used for narration (L1 or L2) mediates hippocampal functional connectivity.

**Cue words:** language, hippocampus, anterior temporal cortex, angular gyrus, body experience

## **Introduction**

Reflection on our own inner experience is typically accompanied by verbal descriptions (Baars et al. 2003). In the present study, we examine inner narratives of past, future, daydream, and self-unrelated, fictitious events, as well as the influence of the language of inner narration on the hippocampo-cortical system. Inner speech, and thus inner narration, develops in late childhood (Alderson-Day and Fernyhough 2015; Fernyhough 2017; Geva and Fernyhough 2019). It plays an important role in metacognition, self-awareness, and self-understanding (Siegrist 1995; Morin and Michaud 2007), as well as creativity (Fernyhough et al. 2008; Langdon et al. 2009), and social understanding (Perrone-Bertolotti et al. 2012; Davis et al. 2013; Alderson-Day and Fernyhough 2014). Inner narration is commonly used when thinking back or forward in time. In many functional magnetic resonance imaging (fMRI) studies on episodic event recall or future-event thinking, it is probable that participants spontaneously use inner narration during the event construction task. Nevertheless, little is known about its contribution to hippocampo-cortical-mediated functions.

The last decade of research on hippocampo-cortical-dependent processing suggests that it involves the construction of a detailed mental representation referred to as an episodic simulation or construction simulation (Ingvar 1985; Atance and O'Neill 2001; Hassabis, Kumaran, and Maguire 2007a; Hassabis and Maguire 2007; Schacter and Addis 2007a; Schacter et al. 2007; Szpunar et al. 2007; Abraham et al. 2008; Botzung, Denkova, and Manning 2008b; Addis et al. 2009; Arzy et al. 2009; Squire et al. 2010; Maguire and Hassabis 2011; Schacter et al. 2012; Szpunar and Schacter 2013; Thakral et al. 2017). More precisely, Maguire and colleagues, in line with

Schacter and Addis's view and findings, highlight that the hippocampal cortical system responds to complex spatial contexts into which event details are bound (Ingvar 1985; Atance and O'Neill 2001; Hassabis, Kumaran, and Maguire 2007a; Hassabis and Maguire 2007; Schacter and Addis 2007a; Schacter et al. 2007; Szpunar et al. 2007; Abraham et al. 2008; Botzung, Denkova, and Manning 2008b; Addis et al. 2009; Arzy et al. 2009; Squire et al. 2010; Maguire and Hassabis 2011; Schacter et al. 2012; Szpunar and Schacter 2013; Thakral et al. 2017). Any spatially coherent fictitious events would entail this process and thus activate the hippocampo-cortical system, such as in daydreams (McCormick et al. 2017, 2018; Spano et al. 2020) and simulated navigation (Hassabis, Kumaran, and Maguire 2007a; Hassabis, Kumaran, Vann, et al. 2007b; Hassabis and Maguire 2007; Schacter and Addis 2007b), which would also be predicted for fictitious events with fictitious characters. In fact, patients with hippocampal damage and a nonfunctional residual hippocampus, cannot construct scenes from autobiographical memory involving spatial navigation, future simulations, or daydreams (Maguire et al. 2016; McCormick et al. 2017, 2018; Spano et al. 2020). This constructive simulation model thus predicts that inner narration of all past, future, daydream, and self-unrelated fictitious events depends on the hippocampo-cortical system (Hassabis, Kumaran, and Maguire 2007a; Hassabis and Maguire 2007; Schacter and Addis 2007a; Addis et al. 2009; Summerfield et al. 2010; Maguire and Hassabis 2011; de Vito et al. 2012; Schacter et al. 2012; Maguire et al. 2016; Dalton et al. 2018; McCormick et al. 2018, 2021). Tulving and colleagues have instead proposed the chronesthesia model, noting that the human sense of time is a necessary component in some types of event construction (Ingvar 1985; Cabeza et al. 1997; Leon and Shadlen 2003; Spreng and Levine 2006; Nyberg et al. 2010; Mullally et al. 2012; Chadwick et al. 2013; Lad et al. 2019; Gauthier et al. 2020). They proposed that only time-locked

event construction—specifying not only “what” and “where” but also “when” events happen—depends on the hippocampo-cortical system. Human beings regularly daydream and construct imaginary events, including self-unrelated, fictitious events, such as those commonly invented in storytelling, that do not involve locating events in specific timeframes (e.g. the past or future). Thus, while such events also involve constructive simulation, they do not involve chronesthesia. These 2 proposed models make different predictions: (i) the constructive simulation model predicts that the inner narration of all past, future, daydream, and self-unrelated, fictitious events depends on the hippocampo-cortical system (construction events) (Hassabis, Kumaran, and Maguire 2007a; Hassabis and Maguire 2007; Schacter and Addis 2007a; Addis et al. 2009; Summerfield et al. 2010; Maguire and Hassabis 2011; de Vito et al. 2012; Schacter et al. 2012; Maguire et al. 2016; Dalton et al. 2018; McCormick et al. 2018, 2021); (ii) Tulving’s chronesthesia model predicts that only the inner narration of past and future (time-locked) events but not daydream or self-unrelated fictitious events will depend on the hippocampo-cortical system (Wheeler et al. 1997; Nyberg et al. 2010). (iii) In addition, we propose a third model, the situated bodily self model, which predicts that inner narration of self-related events which locate the bodily self in space—that is past, future, and daydream but not self-unrelated fictitious events with a fictitious character as the agent of the event—will depend on the hippocampo-cortical system. (iv) Linked to the situated bodily self model, the hippocampo-cortical system could answer to the realness level, i.e. the experience-based level of events, following a decreasing activity with decreasing experience and realness relatedness.

Fluent early bilinguals are able to use inner speech and have access to the semantics of both their languages (Klein et al. 1995; Illes et al. 1999; Abutalebi et al. 2008; Diaz et al. 2008; Abutalebi et al. 2012; Abutalebi et al. 2013; Yang and Yang 2013; Byers-

Heinlein et al. 2017; Prochazka and Vogl 2017). This implies that their inner narrations are formulated in a specific language (either L1 or L2). The inner language used during event narration creates a language context for recall per se (Schrauf and Rubin 2000; Larsen et al. 2002; Matsumoto and Stanny 2006). Previous studies on bilingual episodic autobiographical event recall have been limited to participants who experienced 2 separate monolingual environment periods in their life, such that their memories were marked both by time and language (Schrauf and Rubin 2000; Larsen et al. 2002; Matsumoto and Stanny 2006). Here, we overcame this confound by testing fluent balanced bilinguals who had lived in a bilingual environment from an early age. We controlled the encoding language for each event by using self-related persons (e.g. friends or relatives) with whom the participant only spoke to either in their L1 or L2 as cues for recall. This also enhanced the ecological validity of our study since people naturally chose the appropriate language to use with a specific communicative partner (Martin et al. 2016). In this way, we assured that all in-scanner events cued by a specific person would take place in the same language as all of the events lived and encoded in the interactions with this person (Godden and Baddeley 1975). The language context in inner speech of event construction may influence the system; however, research evidence shows (Oliver et al. 2017) that there are typical differences in phonology and orthography, but differences in semantic are less common. Indeed, here we are using languages (the L1: Basque and the L2: Spanish) that are transparent languages (with a correspondence of phonetics with morphometry) and the differences at the phonological and orthographical levels among them are minimal (Oliver et al. 2017). We thus expect the language context not to differ in terms of neural activity. Whatsoever, the subjective link to the language may affect how the hippocampo-cortical areas interact. The L1 may be seen subjectively as more self-related than the L2 in a bilingual population even

though they live in bilingual contexts. If this is the case in the present population, we can then expect a differential connectivity of the medial prefrontal cortex with the hippocampal body in favor of the L1. Also, the L2 as a more emotionally distanced language might need more access to semantics. Hence, we expect the same areas to be engaged for both languages due to the strict selection of balanced bilinguals, but changes in functional connectivity as a function of the language used are predicted, with the hypothesis that L2 events further strength functional coupling between hippocampal body with semantic regions, while for L1 further strength with self-related regions.

In this research, we used a unique approach that allowed us to consider the influence of narrative context in inner speech description of different types of hippocampus-dependent events. This allowed us to demonstrate that only the inner narration of simulated events involving the bodily self depends on the hippocampo-cortical system. We also illustrated how language choice in bilinguals influences the inner narration of events, with L2 narrations promoting enhanced co-activation of semantic areas and the hippocampus.

## **Material and methods**

### **Participants**

Twenty-nine participants were recruited from the Basque Center on Cognition Brain and Language (BCBL) community and the Gipuzkoa region. Of these, 2 participants were excluded due to excessive in-scanner motion. The final study sample consisted of 27 right-handed participants (14 men, 13 women; mean age  $29.6 \pm 6.4$ ) with Basque as their L1 and Spanish as their L2. They were all early bilinguals (L2 acquired at  $2.2 \pm 2.48$  years of age). This sample was selected because they had lived in a bilingual

context from birth. They experienced everyday exposure to both languages but preferred to use their L1 (see below).

Prior to taking part in the experiment, all participants gave written informed consent in compliance with the ethical regulations established by the BCBL Ethics Committee and the guidelines of the Helsinki Declaration. Participants received monetary compensation for their participation.

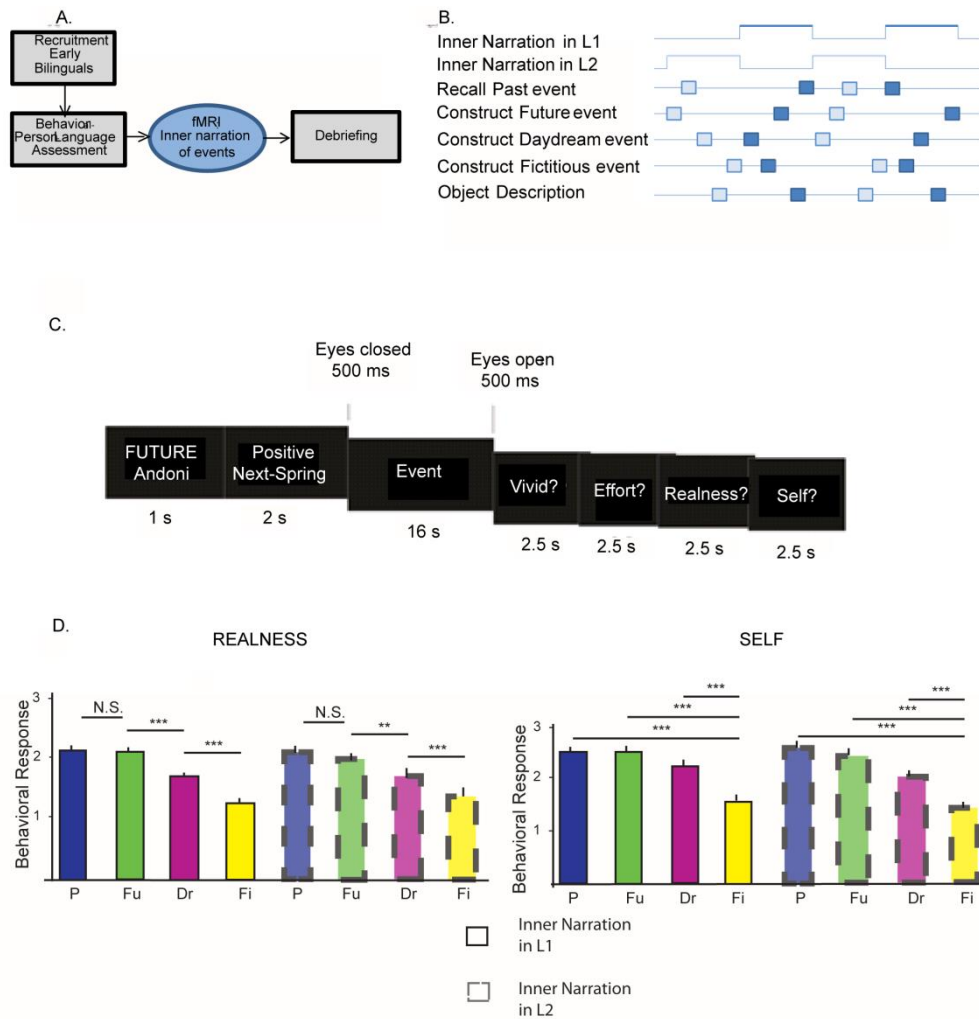
### **Experimental design and procedure**

The procedure comprised 4 steps: (i) “Recruitment”: we recruited early proficient bilinguals, who had acquired their L2 before the age of 6; (ii) “Behavioral assessment before scanning”: our behavioral assessment enabled us to develop self-specific, event type-specific, and language-specific cues for each participant. This procedure allowed us to control the language (L1, L2) of inner speech during encoding to be the same as during the fMRI reconstruction task (see below); (iii) inside the scanner, participants constructed 8 types of “inner narration of events” (4 types in each language) as instructed. Each event type differed in terms of self-relatedness or time dependence; also, event types were carefully chosen to decrease stepwise in terms of realness, depending on how experience-based they were (see Supplementary Table 1A). This was ensured via the instruction, training, and specific cues that were used (see Supplementary Table 1B). The behavioral responses confirmed that the instructions were followed by participants (see Fig. 1D): Specifically, the analysis of variance (ANOVA) on self-relatedness revealed the main effect of Event type ( $F(1.75, 43.74) = 29.405$ ;  $P < 0.001$ ), and no main effect of language ( $F(1, 25) = 2.45$ ;  $P = 0.13$ ) nor an interaction effect ( $F(2.72, 67.89) = 1.06$ ;  $P = 0.37$ ). Self-related past, future, and daydream events being significantly rated more self-related than self-unrelated fictitious



events ( $t > 4.5$ ;  $P < 0.001$ ). On the other hand, the ANOVA on realness also showed a main effect of Event type ( $F(1.575, 39.38) = 35.705$ ;  $P < 0.001$ ), and no language main effect ( $F(1; 25) = 0.06$ ,  $P = 0.81$ ) and an interaction effect ( $F(3, 75) = 2.995$ ;  $P = 0.036$ ). For L1, past and future events were significantly perceived as more real than daydream events ( $t > 5.5$ ;  $P < 0.001$ ), and daydream events were also perceived more real than self-unrelated fictitious events ( $t = 5.4$ ;  $P < 0.001$ ). For L2, past and future events were significantly perceived as more real than daydream events ( $t > 2.5$ ;  $P < 0.018$ ), and daydream events were also perceived more real than self-unrelated fictitious events ( $t = 4.5$ ;  $P < 0.001$ ).

Fig. 1



Experimental design. A) The steps that participants went through included a strict recruitment process; behavioral assessment before scanning to obtain appropriate self and language-specific cues; the scanning tasks; a debriefing. B) Scanning task instructions: A keyword denoting the trial type (“REMEMBER,” “PREVIEW,” “DREAM,” “IMAGINE”) and the first text cue, indicating the scene or object of the visualization and inner narration was presented for 500 ms. Then, a second text cue, indicating the person and time/location of the visualization/inner narration was presented for 3.5 s. Subjects were then instructed to close their eyes and begin visualizing the scene or object while describing it in as much detail as possible using inner speech for the entire 16-s trial duration. A simple audio tone, played through headphones for 1 s, indicated the end of the visualization period, at which point the subject opened their eyes. Subjects then used a 4-button MRI-compatible box to rate their just-narrated scene or object on 5-point scales across 4 dimensions: difficulty, vividness, self-relatedness, and realness. Subjects

were given 3 s to respond per rating. This was followed by a 1-s rest period in which a blank screen was presented before the start of the next trial. Just as in real life, it was the language associated with the cues that indicated of the language of inner speech. C) Overall description of the fMRI design. D) Behavioral results for the ratings on self and realness of events.

Participants also provided a baseline description of an imagined object (cued by the object name) using inner narration in each language. A total of 10 types of trials were assessed (4 constructed event inner narrations and the baseline object inner description in both the L1 and the L2); finally, (iv) the “debriefing” permitted us to assess how participants experienced the event inner narration tasks inside the scanner.

Language proficiency was assessed using both objective and subjective measures. An objective measure of participant proficiency was provided using BEST (de Bruin et al. 2017). Participants’ proficiency was at ceiling in both of their languages and no significant differences between languages ( $P = 1$ ) emerged. Participants also filled in a language background questionnaire where they rated their percentage of exposure to the L1 and the L2 during the last year. Reported use of the L1 during the last year was 63.92% ( $SE = 0.43$ ), whereas the use of the L2 was 43.7% ( $SE = 0.46$ ), revealing a significant preference for the L1 ( $t = 2.338$ ,  $P = 0.027$ ). Finally, participants also rated their emotional connection to their 2 languages on a 10-point visual scale; then, they rated their self-connection to these languages on another 10-point visual analogical scale. This revealed stronger emotional ( $t = 11.938$ ,  $P < 0.001$ ) and self ( $t = 11.04$ ;  $P < 0.001$ ) connection to the L1 (88.57%,  $SE = 0.17$ ; 92.14%,  $SE = 0.14$ ) than the L2 (38.57%,  $SE = 0.38$ ; 42.59%,  $SE = 0.43$ ).

After the language assessment, we asked the participants about people in their lives with whom they could simulate the “self”-related events in the fMRI task. To ensure comparable closeness to persons cueing the L1 and the L2, we asked them to indicate 4

people for each event type (past, future, daydream) in each language, for a total of 24 persons. Participants rated both their emotional relatedness to each person and the extent to which the person they had named formed part of their life on 10-point visual analogical scales. We then computed a “closeness score” by averaging these 2 scores (see Supplementary Table 2). During the procedure, just before scanning, the experimenter selected 2 out of the 4 people the participant had indicated for each event type, thereby ensuring that the level of closeness was as similar as possible for the L1 and L2 within each event type. For the remaining event type (self-unrelated fictitious event), i.e. the least experience based, the experimenter selected culturally familiar fictitious personages (Cyclops, Nymph, Omer-Simpson, Cinderella), with location cues of easily imaginable compositions (e.g. Purple Forest).

### **Cues used to control encoding-language**

Functional MRI scanning was preceded by the behavioral assessment of self-related persons as noted above. By using person-related events, we ensured that the language of encoding would match the language of recall and thus avoided the encoding-retrieval discrepancy effect (Godden and Baddeley 1975). Bilingual studies have shown that people choose to use specific languages based on the person they talk to (Martin et al. 2016). We, therefore, first assessed 4 self-related people with whom the participant spoke only in their L1 and had shared experiences during the last year, and 4 self-related persons with whom the participant spoke only in their L2 and had shared experiences during the last year. For future events, we assessed 4 self-related people with whom the participant spoke only in their L1 and expected to share experiences within the coming year, and 4 self-related people with whom the participant spoke only in their L2 and expected to share experiences within the coming year. For daydream events,

participants selected 4 people (famous people were also acceptable) with whom the participant would only speak in their L1 and would like to daydream about when daydreaming, and 4 people with whom the participant would only speak in their L2 and would like to daydream about when daydreaming. Individuals with similar closeness scores (as described above) were selected for each language. When assessing this a priori selection, we found no significant difference in emotional relatedness ( $t = -0.201$ ,  $P = 0.843$ ) or forming part of their life ( $t = 1.239$ ,  $P = 0.23$ ) scores between the people selected for the L1 and the L2 (see Supplementary Table 2). Also, there was no significant difference in closeness between the L1 and the L2 persons for past, future, and daydream events (see Supplementary Table 2).

In the same vein, past and future persons were not significantly different in closeness ( $t = 1.792$ ;  $P = 0.084$ ) but future and daydream persons and past and daydream persons did differ significantly ( $t = 5.078$ ;  $P < 0.001$ ;  $t = 5.804$ ;  $P < 0.001$ , respectively). Participants were significantly closer to the self-selected past and future persons compared to daydream persons (see Supplementary Table 2).

### **fMRI paradigm**

The fMRI task consisted of 128 inner event narrations. Participants were asked to describe the constructed event with as many details as possible using inner speech in the cued language (L1, L2): what was happening, where they were (or where the fictitious person was), who was there with them (or with the fictitious person), what they felt (or what the fictitious person felt). Each type of event was narrated in only the L1 or the L2. Just as in real life, when the self-related person cue indicated the use of the L1, the participant's subsequent inner speech also had to be in the L1; when the person cue indicated the L2, their inner speech had to be in the L2. Four types of event construction

were assessed: (i) Recalling past events, (ii) previewing future events, (iii) daydreaming events, and (iv) imagining a self-unrelated fictitious event. The participant was given a keyword (“REMEMBER,” “PREVIEW,” “DREAM,” “IMAGINE”) indicating the upcoming event they should visualize and narrate. Then, for each type of event, the participant was given 2 main cues. The first critical cue was a person: a self-related person for past and future events, a self-selected person for daydream events and, as described above, a fictitious person assigned by the experimenter for self-unrelated fictitious events. The second critical cue was a time-tag for past and future events or a place-tag for daydream and self-unrelated fictitious events. Both time and place settings were selected by the experimenter (see Supplementary Table 1B). More precisely, for past and future events, after the keyword prompt, participants were informed which valence, time period, and self-chosen person they should interact with during the event, for example “REMEMBER,” then “negative - past summer - Andoni” or “PREVIEW,” then “positive - next winter - Maite” (past events being real events that have been experienced and future events being realistic events that, taking into account experience, could be predicted to happen). For daydreaming events, cues were real and the participants were asked to compose an event that cannot happen; the valence, place, and specific self-chosen person they would interact with were given after the keyword prompt, for example “DREAM,” then “positive - wonderful beach - Laboa”; for self-unrelated fictitious events, cues were based on fictitious characters and fictitious locations, in addition to the valence of the event. The participants were asked to compose a fictitious event as a story teller would with the given elements. The place and a specific fictitious person that would be the agent of the event were given after the keyword prompt and the valence, for example “IMAGINE,” then “positive - purple forest - Cyclops.” The daydream of the present study is thus quite close to the—self-

related—fictitious events of Hassabis, Kumaran, and Maguire (2007a), while self-unrelated fictitious events are not self-experienced. The advantage of the present studies' setup is to permit a stepwise decrease of realness and experience relatedness between event types. The baseline narration consisted of an inner speech description in the instructed language of an object, displayed against a blank background (to ensure visual input similar to that used in the tasks, the object description was cued by several words, such as “VIEW,” then “blank background - sculpture - clay”; see Fig. 1A–C).

Before the scanner started, participants were informed about the content of the scenes they needed to visualize and narrate, told what type of cues would be provided, and were extensively trained on each type of event in each language using the person cues that had not been selected for the scanner task. Once the task structure was understood, the fMRI scanner task started. To avoid language switching within the same run, language was assessed within blocks. Each run consisted of 2 blocks, one in each language, presented in random order, and composed of 2 past, 2 future, 2 daydream, and 2 self-unrelated fictitious events presented in random order. The order of these L1 or L2 blocks was counterbalanced across participants. The study involved a total of 8 functional runs.

### **MRI data acquisition**

Whole-brain fMRI data acquisition was conducted on a 3-T Siemens Trio TIM whole-body MRI scanner (Siemens Medical Solutions) at the BCBL, using a 32-channel whole-head coil. Snugly fitting headphones (MR Confon) were used to dampen background scanner noise. Participants viewed stimuli backprojected onto a screen with a mirror mounted on the head coil. To limit head movement, the area between a

participant's head and the coil was padded with foam and participants were asked to remain as still as possible.

Functional images were acquired in 8 separate runs using a gradient-echo echo-planar pulse sequence with the following acquisition parameters: time repetition (TR) = 3,000 ms, time echo (TE) = 25 ms, 43 contiguous 3-mm<sup>3</sup> axial slices, no inter-slice gap, flip angle = 90°, field of view (FoV) = 218 mm, 64 × 64 matrix. Prior to each scan, 2 volumes were discarded to allow for T1 equilibration effects. High-resolution MPRAGE T1-weighted structural images were also collected for each participant with the following parameters: TR = 2,300 ms, TE = 2.97 ms; flip angle = 9°, FoV = 256 mm, voxel size = 1 mm<sup>3</sup>, 176 slices.

### **fMRI data analysis**

Standard SPM12 (Wellcome Department of Cognitive Neurology, London) preprocessing routines and analysis methods were employed. Images were corrected for differences in timing of slice acquisition and were realigned to the first volume by means of rigid-body motion transformation.

High-resolution anatomical T1 images and functional volumes were then coregistered and spatially normalized to T1 and echo-planar imaging templates, respectively, to enable anatomical localization of the activations. Templates were based on the MNI305 stereotaxic space (Evans and Collins 1993), an approximation of Talairach space (Talairach and Tournoux 1988). The normalization algorithm used a 12-parameter affine transformation together with a nonlinear transformation involving cosine basis functions. During normalization, the volumes were sampled to 3 mm<sup>3</sup> voxels. Functional volumes were spatially smoothed with an 8-mm full-width at half-maximum isotropic Gaussian kernel.



Statistical analyses were performed on individual participant data using the general linear model (GLM). fMRI time series data were modeled by impulses convolved with a canonical hemodynamic response function (HRF). The motion parameters for translation (i.e. x, y, and z) and rotation (i.e. yaw, pitch, and roll) were included as covariates of non-interest in the GLM. Each trial was modeled as an event, time-locked to the onset of event construction. The resulting functions were used as covariates in a GLM, along with a basic set of cosine functions that high-pass filtered the data, and a covariate for session effects. Contrast images from each subject were submitted to group analyses. At the group level, whole-brain contrasts between conditions were computed by performing a 2 (Language: L1, L2)  $\times$  4 (Event: past, future, daydream, fictitious) ANOVA, treating participants as a random effect. Brain coordinates provided in this text, as well as in the tables and figures, are reported in MNI atlas space (Klein et al. 1995). Not to omit specific nodes of the narrative description of events, we used the t-contrasts for inner narration of past, future, daydream, and self-unrelated fictitious events contrast as a mask and assessed our questions with a  $P < 0.05$  Family-wise error (FWE) voxel-level correction within this mask.

We assessed functional connectivity via the beta-series correlation method (Rissman et al. 2004), implemented in SPM12 with custom Matlab scripts. The canonical HRF in SPM was fit to each occurrence of each condition and the resulting parameter estimates (i.e. beta values) were sorted according to the study conditions to produce a condition-specific beta series for each voxel. Functional connectivity analyses were performed to assess pairwise connectivity between regions of interest (ROIs) within the hippocampocortical system, more specifically, from the left hippocampal body to the middle temporal cortex and from the left hippocampal body to the ventromedial prefrontal cortex (vmPFC).

We used specific masks for the beta-series correlation analysis. We obtained the core network of interest for our ROIs by applying the Neurosynth meta-analytic tool (Yarkoni et al. 2011). We used the term “autobiographical memory” to obtain the maps involved in the core episodic autobiographical network and identified the local maxima in our ROIs: the left anterior temporal cortex (center of mass =  $-62 -8 -16$ ; volume =  $984 \text{ mm}^3$ ) and vmPFC (center of mass =  $0 50 -12$ ; volume =  $984 \text{ mm}^3$ ). We used 6-mm radius spheres in these local maxima for the left anterior temporal cortex and vmPFC. ROI analyses were performed with the MARSBAR toolbox in conjunction with SPM12 (Brett et al. 2002). This meta-analysis also revealed the participation of the left hippocampal body, which, due to its specific shape, was identified anatomically in MNI space (center of mass =  $-27 -28 -9$ ; volume =  $2304 \text{ mm}^3$ ; (Demaster and Ghetti 2013).

Since the correlation coefficient is inherently restricted to range from  $-1$  to  $+1$ , an arc-hyperbolic tangent transform (Fisher 1921) was applied to these beta-series correlation values to make its null hypothesis sampling distribution approach that of the normal distribution. Then, Fisher’s Z normally distributed values were submitted to statistical analysis. To assess the effect of language and event type, we conducted an ANOVA (Language  $\times$  Event) on the hippocampo—anterior-middle-temporal and hippocampal—vmPFC ROI pairs.

## **Results**

### **Behavioral results**

All participants provided in-scanner ratings on a 4-point Likert scale indicating (i) how vividly they experienced each event (vividness score), (ii) how much effort it took to construct the event narration (effort score), (iii) how real the constructed event seemed

(realness score), and (iv) how “self” related the constructed event seemed (self-score). Interestingly, self and realness scores showed a very significant correlation (both the L1 and the L2 events:  $r^2 = 0.775$ ;  $P < 0.001$ ; the L1 events:  $r^2 = 0.695$ ;  $P < 0.001$ ; the L2 events:  $r^2 = 0.739$ ;  $P < 0.001$ ). When assessing the vividness, the ANOVA demonstrated an event type effect ( $F(1.94, 46.62) = 6.397$ ;  $P = 0.004$ ) with a language effect ( $F(1, 24) = 10.35$ ;  $P = 0.004$ ), but no language  $\times$  event interaction ( $F(2.5, 59.93) = 2.449$ ;  $P = 0.083$ ; see Supplementary Fig. 1). This effect was true in the L1 (one-level ANOVA, showed the type of event effect  $F = 8.743$ ;  $P < 0.001$ ) and in the L2 (one-level ANOVA, showed the type of event effect  $F = 5.415$ ;  $P = 0.002$ ).

Also, the level of events’ self-relatedness was correlated with the vividness of events (both the L1 and the L2 events:  $r^2 = 0.437$ ;  $P = 0.026$ ; the L1 events:  $r^2 = 0.428$ ;  $P = 0.029$ ; the L2 events:  $r^2 = 0.313$ ;  $P = 0.127$ ). In the same vein, realness of events was correlated with the vividness of events (both the L1 and the L2 events:  $r^2 = 0.440$ ;  $P = 0.024$ ; the L1 events:  $r^2 = 0.632$ ;  $P = 0.001$ ; the L2 events:  $r^2 = 0.203$ ;  $P = 0.331$ ). On the contrary, effort was not correlated to the vividness of the narrated events ( $r^2 = -0.155$ ;  $P = 0.449$ ).

## **Neuroimaging results**

### **Inner narration of hippocampus-dependent events**

Previous studies using past and future events have shown the involvement of the core episodic-hippocampal system without controlling for the form of recall, that is, whether recall was performed with or without inner speech. This study is unique in terms of the narrative constraints entailed to the silent description with inner speech of the event participants construct. The language used in inner speech gives an inherent context during the event narration in the bilingual population; with such population, we can thus

assess the contextual effect of this inherent context on the event construction. We had constrained participants to describe the constructed events in the L1 or the L2 with inner narration. The t-contrasts for inner narration of past, future, daydream, and self-unrelated fictitious events showed activation in the precuneus–retrosplenial cortex, left and right anterior lateral temporal cortex, the left hippocampal body, and vmPFC (see Supplementary Table 3; also see Supplementary Fig. 2). Thus, when participants were constrained to narrative construction, we observed the recruitment of the core episodic hippocampo-cortical system.

(1) According to the construction simulation model, inner narration of all events should depend on the hippocampo-cortical system. We therefore checked for common activation during inner narration of all types of events in both languages. Surprisingly, common activation for inner narration of past, future, daydream, and self-unrelated fictitious events was only found in the precuneus–retrosplenial cortex for medial regions and in the left and right angular gyri (inferior parietal gyri) for cortical regions (see Fig. 2A and Supplementary Table 3). There was no recruitment of the hippocampus or vmPFC.

(2) According to the chronesthesia model, only inner narration of time-marked events should depend on the hippocampo-cortical system. We checked the common activation for inner narration of events that specified “what,” “where,” and “when,” i.e. inner narration of past and future events. This analysis showed activation of the core episodic hippocampo-cortical system (Hassabis, Kumaran, and Maguire 2007a; Hassabis and Maguire 2007; Abraham et al. 2008; Botzung, Denkova, Ciuciu, et al. 2008a; Botzung, Denkova, and Manning 2008b; Arzy et al. 2009; Spreng et al. 2009; Beaty et al. 2019), including the left hippocampal body, vmPFC, precuneus–retrosplenial cortex, left and right angular gyri, left and right anterior medial temporal gyrus (MTG), and left

temporal pole (see Fig. 2B and Supplementary Table S1). Inner narration of time-locked events was thus associated with the core hippocampo-cortical system in both languages. Surprisingly, when we assessed inner narration of time-locked versus non-time-locked events, only the precuneus–retrosplenial cortex and the left and right angular gyri still showed activation (see Fig. 2D; Supplementary Table 2).

(3) To assess the final hypothesis, that only self-related event narratives linked to experience driven events, depend on the hippocampo-cortical system (Burgess et al. 2001; Maguire 2001; Hassabis, Kumaran, and Maguire 2007a; Hassabis, Kumaran, Vann, et al. 2007b; Hassabis and Maguire 2007; Botzung, Denkova, Ciuciu, et al. 2008a; Spreng et al. 2009; Maguire and Hassabis 2011; de Vito et al. 2012), we restricted our analysis to inner narration of “self” events (whether or not they were time-marked), that is “situated bodily self simulations.” We first assessed common activation with a conjunction analysis for inner narration of past, future, and daydream events (including both the L1 and the L2 event inner narrations). Again, we found activation of the hippocampo-cortical core network (see Fig. 2C; Supplementary Table S1), that is the referential network widely observed in the literature both for past and future event construction (Atance and O'Neill 2001; Spreng and Levine 2006; Hassabis, Kumaran, and Maguire 2007a; Hassabis and Maguire 2007; Schacter et al. 2007; Szpunar et al. 2007; Abraham et al. 2008; Schacter et al. 2008; Maguire and Hassabis 2011; Anderson et al. 2012; de Vito et al. 2012; Schacter et al. 2012; Horner et al. 2016; Beaty et al. 2019): left hippocampal body, vmPFC, precuneus–retrosplenial, left and right angular gyri, left and right anterior MTG, and left temporal pole. Interestingly, when assessing the contrast of inner narration of “self” against “non-self” events, the hippocampo-cortical areas stayed active (see Supplementary Table 4); more precisely, we found a

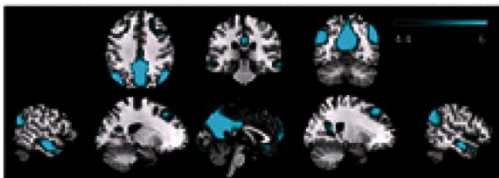
network that included the left hippocampal body, precuneus–retrosplenic cortex, the vmPFC, and anterior inferior temporal cortex (see Fig. 2E).

Fig. 2

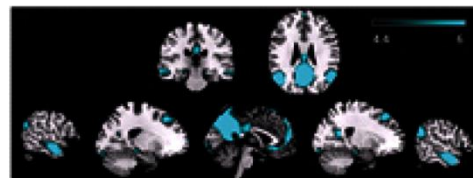
A. Conjunction Construction events



B. Conjunction Time events



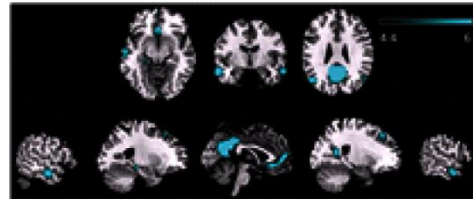
C. Conjunction "Self" events



D. Time events vs. No-Time events



E. "Self" events vs. "No-Self" events

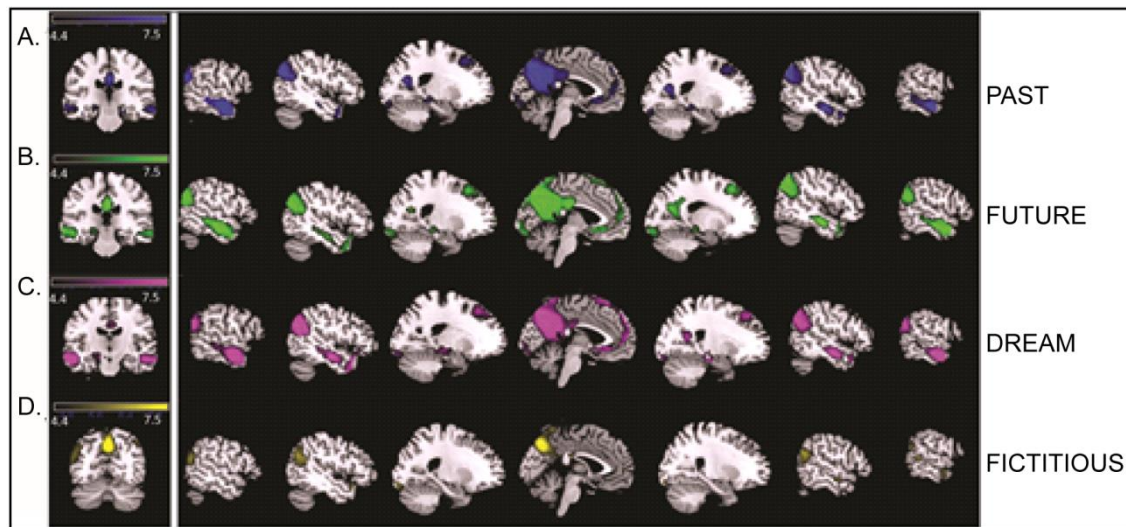


A) The conjunction analysis revealed the brain regions activated by all 4 types of inner event narration. This network included the retrosplenic and posterior parietal cortices, middle temporal cortices, but neither medial prefrontal cortex nor hippocampal areas. B) The conjunction analysis revealed brain regions activated for all time-related events. The core hippocampo-cortical network was engaged. C) The conjunction analysis revealed brain regions activated for all self-related events (regardless of time-tags). The core hippocampo-cortical network was engaged. D) Time events versus non-time events. Only the precuneus–retrosplenic and left and right angular gyri remain. E) The contrast between self events and non-self events. The core hippocampo-cortical network was activated. Views of each distributed brain network are shown at the bottom on a selection of relevant sagittal, coronal, and axial sections from the

averaged structural MRI scan of the 27 subjects, at a threshold of  $P=0.05$  FWE at the voxel level.

We then checked the neural activation of each inner narration event type (see Fig. 3) in greater detail. Most interestingly, inner narration of daydream events showed the exact same core episodic hippocampo-cortical activation even though dreams are not marked by time; just as recent research on sleeping and dreaming based on questionnaires and resting states would suggest (Spano et al. 2020); see Fig. 3C). By contrast, inner narration of self-unrelated fictitious events did not depend on the core hippocampo-cortical neural event, even though it required constructive simulation (see Fig. 3D) and bounding of the event's details in the given context. Note that these self-unrelated fictitious events differ from what were described as fictitious events in the previous literature (which would instead correspond to our (day) dream events). Notably, the agents in our self-unrelated fictitious events were fictitious characters, not the person (participant) constructing the event. This also distinguishes them from navigational and autobiographical scenes.

Fig. 3



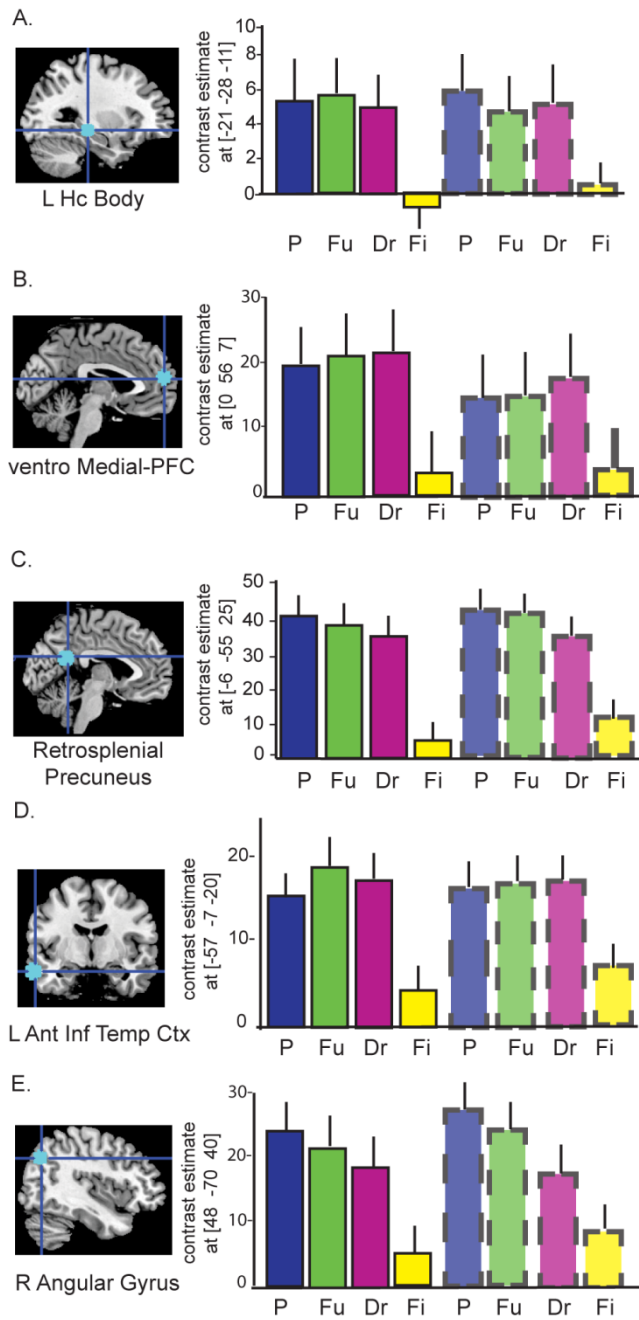
Neural network for each inner event narration: A) Inner narration of past events. B) Inner narration of future events. C) Inner narration of daydream events. D) Inner narration of self-unrelated fictitious events. Views of this distributed brain network are shown at the bottom on a selection of relevant sagittal, coronal, and axial sections from the averaged structural MRI scan of the 27 subjects, at a threshold of  $P = 0.05$  FWE at the voxel level.

#### Language context in inner narration of events

As both languages were expected to be equally semantically accessible, we expected both to engage the ventral pathway of the language system and we did not expect to find any significant effects of language (L1, L2) on the patterns of neural activity. Indeed, we did not find any effect of language due to the use of the L1 or the L2 on inner narration nor any interaction effect. We found only the main effect of event, as described above (Fig. 4A).

Fig. 4





Plots of each area of the hippocampo-cortical system. A) Left hippocampal body (L Hc Body); B) ventromedial prefrontal cortex (vmPFC); C) precuneus–retrosplenial; D) left anterior inferior temporal cortex (L Ant Inf Temp Ctx); E) right (R) angular gyrus. L1: non-dashed dark color; L2: dashed light color.

When plotting activation of the main regions, the right angular gyrus (AG) strictly followed the realness pattern in both the L1 and the L2. Events that had actually been experienced tended to show stronger activation (Fig. 4E). The precuneus–retrosplenial cortex also reflected the level of realness, that is the extent to which an event was experience-based and strongly engaged with in both L1 and L2 (Fig. 4C). Both the AG and retrosplenial cortex answer to the realness level of events. Activity in the left hippocampal body also followed the level of realness associated with narrated events to a certain extent: it reflected how experience-based the narrated event was in L2 but reflected self-relatedness in the L1 (Fig. 4A).

In this sense, the vmPFC showed unexpected involvement in both the L1 and the L2 (Fig. 4B). Of course, the lowest activation was for the non-self fictitious events, but within situated bodily self events, the plot showed the highest activation for inner narration of daydreams: the more oneiric the “self” event the higher the activation in the vmPFC during inner narration. This form of activation was unexpected. The construction that occurs in dream events is based on “self” related semantic elements but has no, for example, limits with regard to time or realness. By contrast, real events such as past and future events are limited by both time and reality. This should constrain narrative constructions based on self-related semantic elements. Anterior MTG was involved in inner narration of all constructed events, even if self-unrelated fictitious events exhibited less activation in both the L1 and the L2 inner narrations (Fig. 4D).

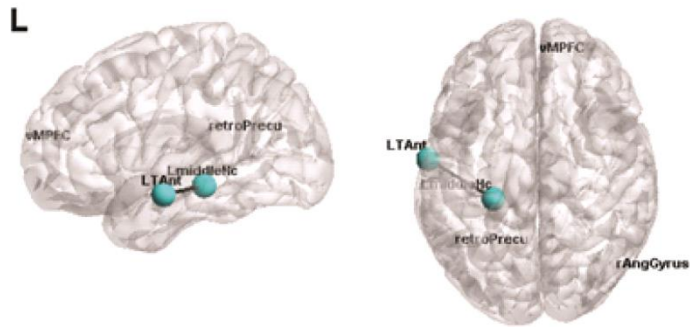
## **Functional connectivity analysis**

### **Hippocampo-anterior temporal cortex**

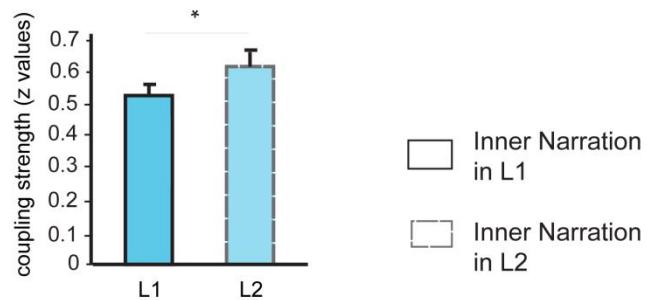
When assessing the functional connectivity of the left hippocampal body, we expected higher intervention from the lateral temporal regions, such as the anterior MTG for inner narration of events in L2 compared to inner narration of events in the L1. Using the beta-series correlation for each event in each language, an Event  $\times$  Language ANOVA revealed an effect of Language ( $F(25)=6.014, P=0.022$ ) but no effect of Event ( $F(25)=0.765, P>0.05$ ) or an Event  $\times$  Language interaction ( $F(25)=2.33, P>0.05$ ). These results suggest that inner narration of events in L2 led to greater functional connectivity between the left hippocampal body and the lateral temporal cortex (see Fig. 5A and B).

Fig. 5

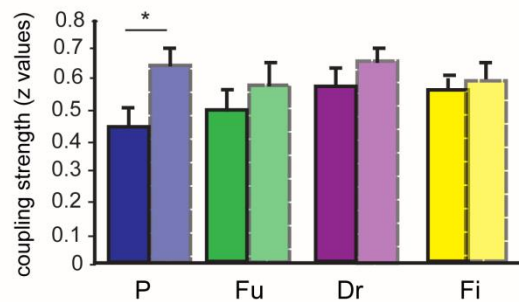
A. L Hc Body - Anterior inferior Temporal Cortex



B.



C.



Beta correlation analysis between left hippocampal body (L Hc Body) and anterior inferior temporal cortex. A) Visual brain representation of functional connectivity. B) Overall language-related plot; dark color, inner speech in the L1; light color, inner speech in the L2. C) Event  $\times$  language plot. Past (P), future (Fu), dream (Dr), self-unrelated fictitious (Fi). Dark color, inner speech in the L1. Light color, inner speech in L2. L1: non-dashed dark color; L2: dashed light color. Asterisks denote statistically significant effects.

We found that only past events drove this effect, with a reliable and significant between Language difference ( $t(25) = -2.759, P = 0.011$ ), while other event types had

nonsignificant impacts (future,  $t(25) = -0.894$ ,  $P > 0.05$ ; daydream,  $t(25) = -1.108$ , fictitious,  $t(25) = -0.441$ ,  $P > 0.05$ ; see Fig. 5C).

### **Hippocampo-medial prefrontal cortex**

As the L1 showed higher “self” scores than L2 (see Section 2), one could hypothesize that inner narration in the L1 boosts connectivity between the left hippocampal body and vmPFC more than inner narration in the L2. However, we did not observe any significant effects in this connectivity between the L1 and the L2.

### **Discussion**

“Thinking is just speaking to ourselves” suggests Kant (1798) (Yarkoni et al. 2011). Indeed, we spontaneously use inner narration when thinking about our past and future experiences. The present paradigm explicitly addressed the hippocampus-dependent event construction process during inner narration in the L1 and the L2. This allowed us to not only characterize the neural system underlying the inner narration of (re)constructed events but to also assess the influence of the language of inner narration.

(i) Despite the fact that all studied event narratives involved construction of a detailed mental representation in space, not all events showed dependence on hippocampo-cortical activation. Instead, the common feature of all event narratives was the involvement of the AG and the precuneus–retrosplenial cortex. This was driven by neural activity related to the inner narration of self-unrelated fictitious events. (ii) The neural network we found active during inner narration of past events (McIntosh et al. 1997; Wheeler et al. 1997; Mullally et al. 2014) and future events (Schacter and Addis 2007a; Beaty et al. 2019) was similar to that endorsed by previous studies of these event constructions and showed the same typical referential hippocampo-cortical dependence. (iii) This typical hippocampo-cortical activity was also evident in the common network

activated by inner narration of all self-related events, including both time-constrained events and daydreaming events with no time-constrain.

Our results suggest that the hippocampal system can be activated regardless of the temporal anchoring of events. The physicist Carlo Rovelli has demonstrated that our naïve linear perception of the flow of time does not correspond to a physical reality but rather to subjective needs (Rovelli 2019). Maguire and Hassabis (2011) have suggested that binding event details to a complex coherent spatial context will always engage the hippocampo-cortical system. The response to daydreaming events' inner narrations, which form part of our oneiric inner life, confirms this prediction, as it also reliably resulted in the activation of the core hippocampo-cortical system but, surprisingly, self-unrelated fictitious events' inner narration did not.

In the present study, it appeared that only “what” and “where” were necessary for eliciting hippocampo-cortical engagement in the 3 types of event constructions. One could say that while self-unrelated fictitious events are also based on “what” and “where,” there is a critical difference when it comes to the “where” aspect. Self-unrelated fictitious events have locations, but they do not involve simulation of a bodily self presence in that location (Bergouignan et al. 2014; Guterstam, Bjornsdotter, Bergouignan, et al. 2015a; Guterstam, Bjornsdotter, Gentile, et al. 2015b; Collins et al. 2017; Bergouignan et al. 2022). That is, the fictitious person, rather than the participant, experiences the event in the given location. For instance, in the self-unrelated fictitious event “Cyclops”+“purple forest,” the participant who constructs the detailed representation of this event does not simulate her/his presence in the purple forest.

Both bodily self-consciousness studies (Bergouignan et al. 2014; Brechet et al. 2018; Gauthier et al. 2020; Bergouignan et al. 2022) and bodily self-location studies

suggest (Guterstam, Bjornsdotter, Bergouignan, et al. 2015a) that the hippocampo-cortical system, and more particularly the hippocampo-parietal complex, to be essential for bodily self-consciousness and self-location in the encoding and retrieval of life events. The simulation of events that include the “self” then triggers the simulation of bodily self-consciousness with a specific self-location that depends on this part of the hippocampo-cortical system.

Aforesaid, we can speculate that the perspective that comes with the events, according to the presence or absence of the bodily self-location simulation, would differ in each event’s type. The self-unrelated fictitious event will most probably be simulated as an outside scene viewer where the fictitious character is seen to act (as most film scenarios, or fictitious stories), which is closer to a third-person perspective of self-events (Bergouignan et al. 2008; St Jacques et al. 2017; Iriye and St Jacques 2020; Bergouignan et al. 2022; Iriye and St Jacques 2021), while the other 3 self-location simulating events may have both first- and third-person perspectives. It would be interesting for future studies to examine the influence of perspective in past, future, daydream, and self-unrelated fictitious events.

Given our findings, and the preceding literature, spatially coherent events, which, as described by past research, are dependent on the hippocampo-cortical system, should include the simulation of the bodily self-location in a spatial context in its definition. Along the same lines, episodic-like memory assessments in animal studies also, predominantly, rely on the “what” and “where” aspects of memory (Jozet-Alves et al. 2013; Igarashi et al. 2014; Horner et al. 2016; Panoz-Brown et al. 2016). Hippocampal place cell studies involve situating the body of the animal in a spatial context that is remembered and will form part of memory content. Of course, this role might not be the unique function of the hippocampal system, as previous work has shown that the

hippocampal system may also be implicated in functions such as object contextualization with no scene representation (McCormick et al. 2018). However, the present study suggests that, in the context of constructed events' inner narration, the human hippocampo-cortical system responds to inner narrations of events that require simulating the bodily self in a specific place. A patient with hippocampal damage due to developmental amnesia (Rosenbaum et al. 2004; Mullally et al. 2014), late epilepsy surgery (Hassabis, Kumaran, Vann, et al. 2007b; Mullally et al. 2012), or specific psychiatric conditions (Bergouignan et al. 2008, 2009, 2011, 2014; Daniels et al. 2012; Nardo et al. 2013; Logue et al. 2018) should, on the one hand, be unable to construct narrations of autobiographical memories nor narrations of simulated spatial navigation, future events, and daydreams; on the other hand, they should reliably have no issues in constructing and narrating fictitious stories with fictitious characters. This hypothesis needs to be tested in these patient populations.

All in all, our results demonstrated that “constructive episodic simulation” is not sufficient, while “chronesthesia” is not mandatory for activation of the hippocampo-cortical system during inner narration of events. It is instead their conjunction in a “simulation of the bodily self in a specific place” that assures involvement of the core hippocampo-cortical system.

On the one hand, the narrative process accompanying inner narration of past, future, and daydream events leads to the classical activation of the hippocampo-cortical neural network. Each area of the neural network responded slightly differently to each event type: the precuneus–retrosplenial, the left hippocampus, the vmPFC, and the AG showed decreasing activation for inner narration of events that had fewer bases in experience, i.e. less realness. For instance, the AG showed a strictly stepwise increasing pattern of activation according to the realness of the constructed event (see Fig. 4E). It



appears that the contribution of the AG was an experience-based (i.e. realness) tag for any inner narration of an event's detailed mental representation.

On the other hand, our data showed that hippocampo-cortical functional coupling was modulated by the language context for the coupling with the anterior lateral inferior temporal cortex but not for the coupling with the vmPFC. There was increased co-activation of the anterior inferior temporal cortex, known to be a semantic area, with the hippocampus hub for inner narration in the L2, specifically for past experienced events. This suggests that the L2 inner narration of events requires a higher level of narrative processing of semantic elements than the L1. Thus, even though our participants live in a bilingual context and are early fluent bilinguals, which should indicate equivalent access to the L1 and the L2 semantics, the choice of inner language still influenced the neural system: the L2 inner speech required greater engagement between a semantic area and the hippocampal body.

In the present paradigm, sentences were silently articulated in the participant's mind in either the L1 or the L2. Most interestingly, during this process, the anterior ITC and both left and right angular gyri were reliably activated for all types of inner event narration. These areas have remained poorly explored in the literature, even though they tend to be present in the core network of the hippocampo-cortical system. Interestingly, bodily self-consciousness appears to share the bilateral AG uniquely with episodic autobiographical memory, i.e. the hippocampo-cortical system, (and not with semantic autobiographical memory). A recent study showed an anatomical overlap bilaterally in the AG, but not in other parietal or temporal lobe structures (Brechet et al. 2018). It would then be interesting to assess whether the present studies' increase with the experience-driven event is also linked to the level of bodily self-consciousness in the event simulation. In parallel, a recent study using transcranial magnetic stimulation

(TMS) (Thakral et al. 2017) revealed that the left AG had a causal role in supporting internal recall of details during an autobiographical memory interview. In the present study, we showed that this area can be engaged even when no autobiographical details are supplied. The AG was active in the conjunction analysis for inner narration of all event types, including self-unrelated fictitious events. Its role might have been enhanced by having to use inner narration in the present study. It followed the realness tag levels from past to future, dream (i.e. self-related fictitious event), to self-unrelated fictitious event (see Fig. 4E), with strictly stepwise increases in activation in accordance with the level of experience. In sum, the AG is activated by any event simulated through inner narration but is increasingly activated the more that event is experience-based.

In any behavioral task of episodic long-term recall, such as the TMS study (Thakral et al. 2017) described above, but also any psychotherapeutic intervention, event construction is accompanied by an event-related narrative (Siegrist 1995; Morin 2009). When the hippocampo-cortical system is studied using functional neuroimaging tools, the participant may also be using inner narration. Episodic autobiographical recall in the scanner, which does not control for the form of recall (with or without inner narration), is thus different from behavioral episodic autobiographical recall, which requires participants to give an event-related narration. The present study makes the first step in addressing the intervention of the narrative processes that take part in the system.

The bilingual population studied here had equal access to the semantics of their 2 languages, although participants had somewhat greater exposure to their L1 and preferred to use it in everyday life. This may point to a limitation of the present study, which is the nonequivalence of exposure to the L1 and the L2. Equal exposure would likely lead to equal connectivity with semantic areas in the hippocampo-cortical system. This limitation could be overcome in future studies by examining linguistic indices not

associated with differences related to exposure or preference. Another limitation could be the intrinsic effect of experience-related cues. As they are experience-based, they are also familiar, then when the cues' realness decreased, the familiarity of cues might decrease. However, the used cues for the self-unrelated events were very familiar characters. Also, although the behavioral data showed less closeness to dream persons compared to persons selected for past or future events, the hippocampo-cortical activity was surprisingly similar to past and future events in dream events (see Figs 3 and 4), which suggests that the neural activity of the present study is not explained by familiarity differences.

This study examined inner narration of events by bilinguals with the aim of assessing the context effect of the used language in inner narration of events and teasing apart the features of hippocampo-cortical system activity. Four main results emerged: (i) The vividness of narrated events follows the self-relatedness and the realness of events, the more the narrated event was self-related or experience-driven the more vivid was the narrated event. (ii) Event-related narration results in core hippocampo-cortical activity but only inner narration of events (without time constraints) that involve simulations of the bodily self in a specific spatial context leads to hippocampal dependency, i.e. binding between the bodily self and a specific place would drive hippocampo-cortical activity; (iii) language context during inner narration of events influences functional connectivity between the hippocampus and semantic areas, showing increased connectivity for L2; and (iv) there is a positive relationship between activity in the AG and the experience-driven reality of events during inner narration.

### **Acknowledgments**

We thank Lars Nyberg for his thoughtful comments; Elger Abrahamse for the interactive discussion on the topic; Magda Altman, James Barry, and Ainhoa Egiguren

for English editing; Joana Izurieta for assistance in recruitment; and David Carcedo for assistance in data collection.

## **Funding**

LB was supported by a grant from the Spanish Ministry of Economy and Competitiveness (MINECO) [RETOS PSI2015-73408-JIN] and a Marie Curie Fellowship. PMP-A was supported by grants from the Spanish Ministry of Science and Innovation [RYC-2014-15440; PGC2018-093408-B-I00], Neuroscience projects from the Fundación Tatiana Pérez de Guzmán el Bueno, Basque Government [PIBA-2021-1-0003], and a grant from “la Caixa” Banking Foundation under the project code LCF/PR/HR19/52160002. This research was carried out at the Basque Center on Cognition Brain and Language, which is supported by funding from the Basque Government through the BERC 2022-2025 program and by the Spanish State Research Agency through BCBL Severo Ochoa excellence accreditation CEX2020-001010-S.

## **Conflict of interest statement**

The authors declare no conflicts of interest.

## **References**

- Abraham A, Schubotz RI, von Cramon DY. Thinking about the future versus the past in personal and non-personal contexts. *Brain Res.* 2008;1233:106–119.
- Abutalebi J, Annoni JM, Zimine I, Pegna AJ, Seghier ML, Lee-Jahnke H, Lazeyras F, Cappa SF, Khateb A. Language control and lexical competition in bilinguals: an event-related fMRI study. *Cereb Cortex.* 2008;18(7):1496–1505.

- Abutalebi J, Della Rosa PA, Green DW, Hernandez M, Scifo P, Keim R, Cappa SF, Costa A. Bilingualism tunes the anterior cingulate cortex for conflict monitoring. *Cereb Cortex*. 2012;22(9):2076–2086.
- Abutalebi J, Della Rosa PA, Gonzaga AK, Keim R, Costa A, Perani D. The role of the left putamen in multilingual language production. *Brain Lang*. 2013;125(3):307–315.
- Addis DR, Pan L, Vu MA, Laiser N, Schacter DL. Constructive episodic simulation of the future and the past: distinct subsystems of a core brain network mediate imagining and remembering. *Neuropsychologia*. 2009;47(11):2222–2238.
- Alderson-Day B, Fernyhough C. More than one voice: investigating the phenomenological properties of inner speech requires a variety of methods. *Conscious Cogn*. 2014;24:113–114.
- Alderson-Day B, Fernyhough C. Inner speech: development, cognitive functions, phenomenology, and neurobiology. *Psychol Bull*. 2015;141(5):931–965.
- Anderson RJ, Dewhurst SA, Nash RA. Shared cognitive processes underlying past and future thinking: the impact of imagery and concurrent task demands on event specificity. *J Exp Psychol Learn Mem Cogn*. 2012;38(2):356–365.
- Arzy S, Collette S, Ionta S, Fornari E, Blanke O. Subjective mental time: the functional architecture of projecting the self to past and future. *Eur J Neurosci*. 2009;30(10):2009–2017.
- Atance CM, O’Neill DK. Episodic future thinking. *Trends Cogn Sci*. 2001;5(12):533–539.

- Baars BJ, Ramsay TZ, Laureys S. Brain, conscious experience and the observing self. *Trends Neurosci.* 2003;26(12):671–675.
- Beaty RE, Seli P, Schacter DL. Thinking about the past and future in daily life: an experience sampling study of individual differences in mental time travel. *Psychol Res.* 2019;83(4):805–816.
- Bergouignan L, Lemogne C, Foucher A, Longin E, Vistoli D, Allilaire JF, Fossati P. Field perspective deficit for positive memories characterizes autobiographical memory in euthymic depressed patients. *Behav Res Ther.* 2008;46(3):322–333.
- Bergouignan L, Chupin M, Czechowska Y, Kinkingnehun S, Lemogne C, Le Bastard G, Lepage M, Garnero L, Colliot O, Fossati P. Can voxel based morphometry, manual segmentation and automated segmentation equally detect hippocampal volume differences in acute depression? *NeuroImage.* 2009;45(1):29–37.
- Bergouignan L, Lefranc JP, Chupin M, Morel N, Spano JP, Fossati P. Breast cancer affects both the hippocampus volume and the episodic autobiographical memory retrieval. *PLoS One.* 2011;6(10):e25349.
- Bergouignan L, Nyberg L, Ehrsson HH. Out-of-body-induced hippocampal amnesia. *Proc Natl Acad Sci U S A.* 2014;111(12): 4421–4426.
- Bergouignan L, Nyberg L, Ehrsson HH. Out-of-body memory encoding causes third-person perspective at recall. *J Cogn Psychol.* 2022;34(1):160–178.
- Botzung A, Denkova E, Ciuciu P, Scheiber C, Manning L. The neural bases of the constructive nature of autobiographical memories studied with a self-paced fMRI design. *Memory.* 2008a;16(4): 351–363.

- Botzung A, Denkova E, Manning L. Experiencing past and future personal events: functional neuroimaging evidence on the neural bases of mental time travel. *Brain Cogn.* 2008b;66(2): 202–212.
- Brechet L, Grivaz P, Gauthier B, Blanke O. Common recruitment of angular gyrus in episodic autobiographical memory and bodily self-consciousness. *Front Behav Neurosci.* 2018;12:270.
- Brett M, Anton JL, Valabregue R, P. J.B. Region of interest analysis using an SPM toolbox. *NeuroImage.* 2002;16(2):497.
- de Bruin A, Carreiras M, Dunabeitia JA. The BEST dataset of language proficiency. *Front Psychol.* 2017;8:522.
- Burgess N, Maguire EA, Spiers HJ, O’Keefe J. A temporoparietal and prefrontal network for retrieving the spatial context of lifelike events. *NeuroImage.* 2001;14(2):439–453.
- Byers-Heinlein K, Morin-Lessard E, Lew-Williams C. Bilingual infants control their languages as they listen. *Proc Natl Acad Sci U S A.* 2017;114(34):9032–9037.
- Cabeza R, Grady CL, Nyberg L, McIntosh AR, Tulving E, Kapur S, Jennings JM, Houle S, Craik FI. Age-related differences in neural activity during memory encoding and retrieval: a positron emission tomography study. *J Neurosci.* 1997;17(1):391–400.
- Chadwick MJ, Mullally SL, Maguire EA. The hippocampus extrapolates beyond the view in scenes: an fMRI study of boundary extension. *Cortex.* 2013;49(8):2067–2079.

- Collins KL, Guterstam A, Cronin J, Olson JD, Ehrsson HH, Ojemann JG. Ownership of an artificial limb induced by electrical brain stimulation. *Proc Natl Acad Sci U S A*. 2017;114(1):166–171.
- Dalton MA, Zeidman P, McCormick C, Maguire EA. Differentiable processing of objects, associations, and scenes within the hippocampus. *J Neurosci*. 2018;38(38):8146–8159.
- Daniels JK, Coupland NJ, Hegadoren KM, Rowe BH, Densmore M, Neufeld RW, Lanius RA. Neural and behavioral correlates of peritraumatic dissociation in an acutely traumatized sample. *J Clin Psychiatry*. 2012;73(4):420–426.
- Davis PE, Meins E, Fernyhough C. Individual differences in children's private speech: the role of imaginary companions. *J Exp Child Psychol*. 2013;116(3):561–571.
- DeMaster DM, Ghetti S. Developmental differences in hippocampal and cortical contributions to episodic retrieval. *Cortex*. 2013;49(6): 1482–1493.
- Diaz B, Baus C, Escera C, Costa A, Sebastian-Galles N. Brain potentials to native phoneme discrimination reveal the origin of individual differences in learning the sounds of a second language. *Proc Natl Acad Sci U S A*. 2008;105(42):16083–16088.
- Evans A, Collins K. A 305-member MRI-based stereotactic atlas for CBF activation studies. In: *Proceedings of the 40th Annual Meeting of the Society for Nuclear Medicine*. Toronto, Canada; 1993
- Fernyhough C. Talking to ourselves. *Sci Am*. 2017;317(2):74–79.



Fernyhough C, Jones SR, Whittle C, Waterhouse J, Bentall RP. Theory of mind, schizotypy, and persecutory ideation in young adults. *Cogn Neuropsychiatry*. 2008;13(3):233–249.

Fisher R. On the 'probable error' of a coefficient of correlation deduced from a small sample. *Metron*. 1921;1:1–32.

Gauthier B, Brechet L, Lance F, Mange R, Herbelin B, Faivre N, Bolton TAW, Ville DV, Blanke O. First-person body view modulates the neural substrates of episodic memory and auto-noetic consciousness: a functional connectivity study. *NeuroImage*. 2020;223:117370.

Geva S, Fernyhough C. A penny for your thoughts: children's inner speech and its neuro-development. *Front Psychol*. 2019;10:1708.

Godden DRB, Baddeley AD. Context-dependent memory in two natural environments: on land and underwater. *Br J Psychol*. 1975;66(3): 325–331.

Guterstam A, Bjornsdotter M, Bergouignan L, Gentile G, Li TQ, Ehrsson HH. Decoding illusory self-location from activity in the human hippocampus. *Front Hum Neurosci*. 2015a;9:412.

Guterstam A, Bjornsdotter M, Gentile G, Ehrsson HH. Posterior cingulate cortex integrates the senses of self-location and body ownership. *Curr Biol*. 2015b;25(11):1416–1425.

Hassabis D, Maguire EA. Deconstructing episodic memory with construction. *Trends Cogn Sci*. 2007;11(7):299–306.

- Hassabis D, Kumaran D, Maguire EA. Using imagination to understand the neural basis of episodic memory. *J Neurosci*. 2007a;27(52):14365–14374.
- Hassabis D, Kumaran D, Vann SD, Maguire EA. Patients with hippocampal amnesia cannot imagine new experiences. *Proc Natl Acad Sci U S A*. 2007b;104(5):1726–1731.
- Horner AJ, Bisby JA, Zotow E, Bush D, Burgess N. Grid-like processing of imagined navigation. *Curr Biol*. 2016;26(6):842–847.
- Igarashi KM, Lu L, Colgin LL, Moser MB, Moser EI. Coordination of entorhinal-hippocampal ensemble activity during associative learning. *Nature*. 2014;510(7503):143–147.
- Illes J, Francis WS, Desmond JE, Gabrieli JD, Glover GH, Poldrack R, Lee CJ, Wagner AD. Convergent cortical representation of semantic processing in bilinguals. *Brain Lang*. 1999;70(3):347–363.
- Ingvar DH. "Memory of the future": an essay on the temporal organization of conscious awareness. *Hum Neurobiol*. 1985;4(3):127–136.
- Iriye H, St Jacques PL. How visual perspective influences the spatiotemporal dynamics of autobiographical memory retrieval. *Cortex*. 2020;129:464–475.
- Iriye H, St Jacques PL. Memories for third-person experiences in immersive virtual reality. *Sci Rep*. 2021;11(1):4667.
- Jozet-Alves C, Bertin M, Clayton NS. Evidence of episodic-like memory in cuttlefish. *Curr Biol*. 2013;23(23):R1033–R1035.
- Kant I. *Anthropologie in pragmatischer hinsicht*. Königsberg: F. Nicolovius; 1798

- Klein D, Milner B, Zatorre RJ, Meyer E, Evans AC. The neural substrates underlying word generation: a bilingual functional imaging study. *Proc Natl Acad Sci U S A*. 1995;92(7):2899–2903.
- Lad M, Mullally SL, Houston AL, Kelly T, Griffiths TD. Characterizing memory loss in patients with autoimmune limbic encephalitis hippocampal lesions. *Hippocampus*. 2019;29(11):1114–1120.
- Langdon R, Jones SR, Connaughton E, Fernyhough C. The phenomenology of inner speech: comparison of schizophrenia patients with auditory verbal hallucinations and healthy controls. *Psychol Med*. 2009;39(4):655–663.
- Larsen SF, Schrauf RW, Fromholt P, Rubin DC. Inner speech and bilingual autobiographical memory: a Polish-Danish cross-cultural study. *Memory*. 2002;10(1):45–54.
- Leon MI, Shadlen MN. Representation of time by neurons in the posterior parietal cortex of the macaque. *Neuron*. 2003;38(2):317–327.
- Logue MW, van Rooij SJH, Dennis EL, Davis SL, Hayes JP, Stevens JS, Densmore M, Haswell CC, Ipser J, Koch SBJ, et al. Smaller hippocampal volume in posttraumatic stress disorder: a multisite ENIGMA-PGC study: subcortical volumetry results from posttraumatic stress disorder consortia. *Biol Psychiatry*. 2018;83(3): 244–253.
- Maguire EA. Neuroimaging studies of autobiographical event memory. *Philos Trans R Soc Lond Ser B Biol Sci*. 2001;356(1413):1441–1451.
- Maguire EA, Hassabis D. Role of the hippocampus in imagination and future thinking. *Proc Natl Acad Sci U S A*. 2011;108(11):E39.

- Maguire EA, Intraub H, Mullally SL. Scenes, spaces, and memory traces: what does the hippocampus do? *Neuroscientist*. 2016;22(5): 432–439.
- Martin CD, Molnar M, Carreiras M. The proactive bilingual brain: using interlocutor identity to generate predictions for language processing. *Sci Rep*. 2016;6:26171.
- Matsumoto A, Stanny CJ. Language-dependent access to autobiographical memory in Japanese-English bilinguals and US monolinguals. *Memory*. 2006;14(3):378–390.
- McCormick C, Rosenthal CR, Miller TD, Maguire EA. Deciding what is possible and impossible following hippocampal damage in humans. *Hippocampus*. 2017;27(3):303–314.
- McCormick C, Rosenthal CR, Miller TD, Maguire EA. Mind-wandering in people with hippocampal damage. *J Neurosci*. 2018;38(11): 2745–2754.
- McCormick C, Dalton MA, Zeidman P, Maguire EA. Characterising the hippocampal response to perception, construction and complexity. *Cortex*. 2021;137:1–17.
- McIntosh AR, Nyberg L, Bookstein FL, Tulving E. Differential functional connectivity of prefrontal and medial temporal cortices during episodic memory retrieval. *Hum Brain Mapp*. 1997;5(4): 323–327.
- Morin A. Self-awareness deficits following loss of inner speech: Dr. Jill Bolte Taylor's case study. *Conscious Cogn*. 2009;18(2): 524–529.
- Morin A, Michaud J. Self-awareness and the left inferior frontal gyrus: inner speech use during self-related processing. *Brain Res Bull*. 2007;74(6):387–396.
- Mullally SL, Hassabis D, Maguire EA. Scene construction in amnesia: an FMRI study. *J Neurosci*. 2012;32(16):5646–5653.

- Mullally SL, Vargha-Khadem F, Maguire EA. Scene construction in developmental amnesia: an fMRI study. *Neuropsychologia*. 2014;52:1–10.
- Nardo D, Hogberg G, Lanius RA, Jacobsson H, Jonsson C, Hallstrom T, Pagani M. Gray matter volume alterations related to trait dissociation in PTSD and traumatized controls. *Acta Psychiatr Scand*. 2013;128(3):222–233.
- Nyberg L, Kim AS, Habib R, Levine B, Tulving E. Consciousness of subjective time in the brain. *Proc Natl Acad Sci U S A*. 2010;107(51): 22356–22359.
- Oliver M, Carreiras M, Paz-Alonso PM. Functional dynamics of dorsal and ventral reading networks in bilinguals. *Cereb Cortex*. 2017;27(12):5431–5443.
- Panoz-Brown D, Corbin HE, Dalecki SJ, Gentry M, Brotheridge S, Sluka CM, Wu JE, Crystal JD. Rats remember items in context using episodic memory. *Curr Biol*. 2016;26(20):2821–2826.
- Perrone-Bertolotti M, Kujala J, Vidal JR, Hamame CM, Ossandon T, Bertrand O, Minotti L, Kahane P, Jerbi K, Lachaux JP. How silent is silent reading? Intracerebral evidence for top-down activation of temporal voice areas during reading. *J Neurosci*. 2012;32(49): 17554–17562.
- Prochazka K, Vogl G. Quantifying the driving factors for language shift in a bilingual region. *Proc Natl Acad Sci U S A*. 2017;114(17): 4365–4369.
- Rissman J, Gazzaley A, D’Esposito M. Measuring functional connectivity during distinct stages of a cognitive task. *NeuroImage*. 2004;23(2):752–763.
- Rosenbaum RS, McKinnon MC, Levine B, Moscovitch M. Visual imagery deficits, impaired strategic retrieval, or memory loss: disentangling the nature of an amnesic

person's autobiographical memory deficit. *Neuropsychologia*. 2004;42(12): 1619–1635.

Rovelli C. *The order of time*. New York (NY): Riverhead Books; 2019 Schacter DL, Addis DR. The cognitive neuroscience of constructive memory: remembering the past and imagining the future. *Philos Trans R Soc Lond Ser B Biol Sci*. 2007a;362(1481): 773–786.

Schacter DL, Addis DR. Constructive memory: the ghosts of past and future. *Nature*. 2007b;445(7123):27.

Schacter DL, Addis DR, Buckner RL. Remembering the past to imagine the future: the prospective brain. *Nat Rev Neurosci*. 2007;8(9): 657–661.

Schacter DL, Addis DR, Buckner RL. Episodic simulation of future events: concepts, data, and applications. *Ann N Y Acad Sci*. 2008;1124:39–60.

Schacter DL, Addis DR, Hassabis D, Martin VC, Spreng RN, Szpunar KK. The future of memory: remembering, imagining, and the brain. *Neuron*. 2012;76(4):677–694.

Schrauf RW, Rubin DC. Internal languages of retrieval: the bilingual encoding of memories for the personal past. *Mem Cogn*. 2000;28(4):616–623.

Siegrist M. Inner speech as a cognitive process mediating selfconsciousness and inhibiting self-deception. *Psychol Rep*. 1995;76(1):259–265.

Spano G, Pizzamiglio G, McCormick C, Clark IA, De Felice S, Miller TD, Edgin JO, Rosenthal CR, Maguire EA. Dreaming with hippocampal damage. *elife*. 2020;9:e56211.

- Spreng RN, Levine B. The temporal distribution of past and future autobiographical events across the lifespan. *Mem Cogn*. 2006;34(8):1644–1651.
- Spreng RN, Mar RA, Kim AS. The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. *J Cogn Neurosci*. 2009;21(3):489–510.
- Squire LR, van der Horst AS, McDuff SG, Frascino JC, Hopkins RO, Mauldin KN. Role of the hippocampus in remembering the past and imagining the future. *Proc Natl Acad Sci U S A*. 2010;107(44): 19044–19048.
- St Jacques PL, Szpunar KK, Schacter DL. Shifting visual perspective during retrieval shapes autobiographical memories. *NeuroImage*. 2017;148:103–114.
- Summerfield JJ, Hassabis D, Maguire EA. Differential engagement of brain regions within a 'core' network during scene construction. *Neuropsychologia*. 2010;48(5):1501–1509.
- Szpunar KK, Schacter DL. Get real: effects of repeated simulation and emotion on the perceived plausibility of future experiences. *J Exp Psychol Gen*. 2013;142(2):323–327.
- Szpunar KK, Watson JM, McDermott KB. Neural substrates of envisioning the future. *Proc Natl Acad Sci U S A*. 2007;104(2): 642–647.
- Talairach J, Tournoux P. Co-planar stereotactic atlas of the human brain. Stuttgart/New York: Thieme; 1988

Thakral PP, Benoit RG, Schacter DL. Imagining the future: the core episodic simulation network dissociates as a function of timecourse and the amount of simulated information. *Cortex*. 2017;90: 12–30.

de Vito S, Gamboz N, Brandimonte MA, Barone P, Amboni M, Della Sala S. Future thinking in Parkinson's disease: an executive function? *Neuropsychologia*. 2012;50(7):1494–1501.

Wheeler MA, Stuss DT, Tulving E. Toward a theory of episodic memory: the frontal lobes and autonoetic consciousness. *Psychol Bull*. 1997;121(3):331–354.

Yang S, Yang H. Does bilingual fluency moderate the disruption effect of cultural cues on second-language processing? *Proc Natl Acad Sci U S A*. 2013;110(47):E4403.

Yarkoni T, Poldrack RA, Nichols TE, Van Essen DC, Wager TD. Large-scale automated synthesis of human functional neuroimaging data. *Nat Methods*. 2011;8(8):665–670.