Out-of-body–induced hippocampal amnesia

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Edited* by Endel Tulving, retired, Toronto, Canada, and approved February 7, 2014 (received for review October 4, 2013)

Theoretical models have suggested an association between the ongoing experience of the world from the perspective of one's own body and hippocampus-based episodic memory. This link has been supported by clinical reports of long-term episodic memory impairments in psychiatric conditions with dissociative symptoms, in which individuals feel detached from themselves as if having an out-of-body experience. Here, we introduce an experimental approach to examine the necessary role of perceiving the world from the perspective of one's own body for the successful episodic encoding of real-life events. While participants were involved in a social interaction, an out-of-body illusion was elicited, in which the sense of bodily self was displaced from the real body to the other end of the testing room. This condition was compared with a well-matched in-body illusion condition, in which the sense of bodily self was colocalized with the real body. In separate recall sessions, performed ∼1 wk later, we assessed the participants' episodic memory of these events. The results revealed an episodic recollection deficit for events encoded out-of-body compared with in-body. Functional magnetic resonance imaging indicated that this impairment was specifically associated with activity changes in the posterior hippocampus. Collectively, these findings show that efficient hippocampus-based episodic-memory encoding requires a first-person perspective of the natural spatial relationship between the body and the world. Our observations have important implications for theoretical models of episodic memory, neurocognitive models of self, embodied cognition, and clinical research into memory deficits in psychiatric disorders.

self-consciousness | body illusion | dissociative experience | autobiographical memory

Humans have the capacity to "travel back in time" and reexperience past events of their lives. This capacity to retrieve the "what, where, and when" of rich autobiographical memories is based on the episodic memory system (1), and it has been associated with key brain regions, such as the hippocampus (2–8). A characteristic feature of episodic memory is its intimate link with one's "self" (1, 9–11). There is always an "I" that experiences the original event and an I that reexperiences the event during the act of remembering. However, it has not been possible to investigate this fundamental connection between episodic memory and the "I experience" empirically because experimental paradigms for manipulating the perceptual sense of I in space have only recently been developed (12–14) (see further below).

A core feature of the "I experience" is a continuing experience of the self as a distinguishable physical entity centered within the body ("sense of bodily self"). This experience, distinct from the external world, represents the most basic aspect of self-consciousness (14–16). Every event in our lives is experienced from the natural perspective of our own bodies. This first-person perspective constitutes the default mode of information processing in human cognition and defines the egocentric spatial reference frame that is fundamental for spatial perception, action, and cognition. A key function of the hippocampus is binding ongoing sensory, cognitive, and emotional information into coherent representations for long-term storage (4, 7, 17–19). The cortical information is transmitted to the hippocampus, which transforms these ongoing life experiences into long-term memories. Then, during recall, the hippocampus supports the reactivation of the same cortical and subcortical networks. Damage to the hippocampus selectively affects the experiential quality of episodic memory (20). A fundamental assumption in theories and experiments on hippocampal-based episodic memory (1, 9, 10, 21) that, to the best our knowledge, has never formally been tested is the necessity to perceive an event from a first-person perspective centered on the body for the information to be encoded optimally.

Qualitative evidence for a link between the episodic memory system and the body-centered first-person perspective has come from clinical reports. Impairments in the ability to retrieve life events are seen in disorders with dissociative symptoms, in which individuals report feeling detached from themselves or outside of their own bodies [e.g., posttraumatic stress disorder (22), borderline disorder (23), and schizophrenia (24)]. For instance, patients with posttraumatic stress disorder often report experiencing acutely traumatic events from a location outside of their bodies (25), and they have reduced ability to remember the traumatic event (26). These and related clinical observations suggest that disturbances in the default way of experiencing the world from the perspective of one's own body affect subsequent memory of these experiences.

We took advantage of recent developments in the cognitive neuroscience of bodily self-perception (12–14) to induce "an out-of-body dissociative experience" in healthy humans experiencing real-life events (Fig. 1), and we examined whether they would later display impaired episodic memory of these events. With the assistance of a professional actor, we created ecologically valid, socially and emotionally challenging events that the participants could remember vividly 1 wk later (see *SI Paradigm Development*

Significance

Transformation of experiences into long-term memory is a remarkable capability. However, some experiences are so extreme that they are not translated into coherent or lasting memories. Clinical reports suggest that one potential mechanism for memory disturbance could be "dissociative experiences," in which events are experienced in a distance from the body (out-of-body). Here, we experimentally induced an illusory out-of-body experience on healthy participants while they were experiencing life events. Remarkably, participants had an episodic impairment for events encoded out-of-body. Out-of-body encoding specifically impacted the activation of the left posterior hippocampus during retrieval. These findings establish that hippocampus-based episodic memory depends on the perception of the world from within one's own body, and that a dissociative experience during encoding blocks the memory-forming mechanism.

Author contributions: L.B., L.N., and H.H.E. designed research; L.B. performed research; L.B. analyzed data; and L.B., L.N., and H.H.E. wrote the paper.

The authors declare no conflict of interest.

*This Direct Submission article had a prearranged editor.

Freely available online through the PNAS open access option.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1318801111/-/DCSupplemental.

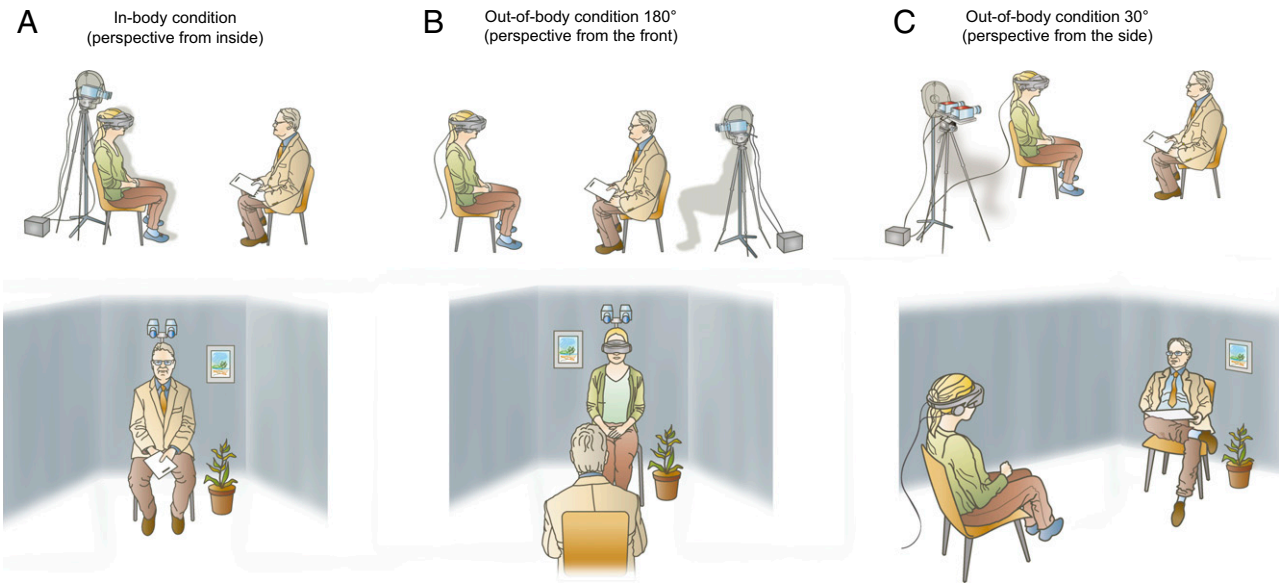

Fig. 1. Schematic representation of the experimental setup used during life event encoding. Manipulation of the experienced self-location (shaded figure) relative to the real body (filled figure with HMDs), in three experimental conditions during a social interaction with a professor (an actor; filled figure with the suit). View from the side (*Upper*) and view from the HMDs (*Lower*), i.e., the view of the participant. (*A*) The in-body condition; (*B*) the out-of-body condition at 180°; and (*C*) the out-of-body condition at 30°.

Exp. 1). The crucial experimental manipulation was to use a multisensory full-body illusion to move the center of bodily and spatial awareness (sense of bodily self) from the location of the real body to the other end of the testing room such that the test individual experienced the life event from outside her/his body (12). We compared this condition to a well-matched control condition, in which the sense of bodily self was placed in a very similar location as the real body such that the test individual experienced the event from within the body.

We predicted that life events encoded with the sense of the bodily self displaced outside the real body would disturb the hippocampo-cortical episodic system and elicit a deficit in long-term memory, compared with events encoded in the in-body condition. We expected the hippocampal binding mechanism to work optimally for events encoded in the in-body condition, in which all of the information to be encoded was presented from the in-body first-person perspective, and that violations to this default mode would impair hippocampal functioning. The results obtained from behavioral and functional magnetic resonance imaging (fMRI) studies have provided experimental support for these predictions, thus yielding compelling evidence for the basic dependence of the hippocampal episodic system on the first-person in-body perceptual experience of the world.

Results

Experimental Out-of-Body Dissociative Experience. During the life events to be remembered ("encoding sessions"), the participants sat in a chair and wore a set of head-mounted displays (HMDs) and earphones, which were connected to two closed-circuit television (CCTV) cameras and to an advanced "dummy-head microphone," respectively. This technology enabled the participants to see and hear the testing room in three dimensions from the perspective of the cameras mounted with the dummy head microphones (Fig. 1). The cameras were either placed immediately above and behind the actual head of the participant, creating an experience of the room from the perspective of the real body (in-body condition), or the cameras were placed 2 m in front [experiment (exp.) 1] or to the side (exp. 2) of the participant, thus making the participants experience the room and the individuals in it as an observer outside of their real body (out-of-body condition). To induce the strong illusion of being fully located in one of these two locations and sensing an illusory body in this place (12, 27), we repetitively moved a rod toward a location below the cameras and synchronously touched the participant's chest for a period of 70 s, which provided congruent multisensory stimulation to elicit illusory perceptions (12). The illusion was maintained for 5 min, during which the ecologically valid life events took place (see next section); throughout this period, the participant received spatially congruent visual and auditory information via the synchronized HMDs and dummy head microphones, which further facilitated the maintenance of the illusion (*SI Paradigm Development Exp. 2*).

Life Events-Encoding Sessions. The life events to be remembered consisted of an oral examination for which the participants had to prepare by reading written material (*SI Materials and Methods*). The eccentric professor conducting the examination was, unbeknownst to the participant, a professional actor who was following a script to create a realistic and natural social interaction, while still controlling the contents of the complex experience. The experiment started when the participant was led into the testing room; the participants were seated and equipped with the HMDs, and the full-body illusion was induced as described in the preceding paragraph (in-body or out-of-body conditions). The "professor" (i.e., the actor) entered the room and the field of view of the HMDs. The professor sat in front of the participant's real body and interacted verbally with him or her for ∼5 min, sometimes standing next to the chair (the illusion was maintained; *SI Paradigm Development Exp. 2* and Fig. S1). The participant was allowed to respond verbally but was instructed to sit still to preserve the illusion. Each oral examination consisted of general questions and monologues intermingled with oral examination questions that assessed the participants' knowledge on each examination topic. The script was based on a classical theater piece, and all of the participants were students to enhance the self-relevance of the event (see *SI Materials and Methods* for further details about the experimental procedures). After each oral examination (or "life event"), the professor left the room, and there was a short break, during which the experimenter entered the room and collected questionnaire data quantifying the

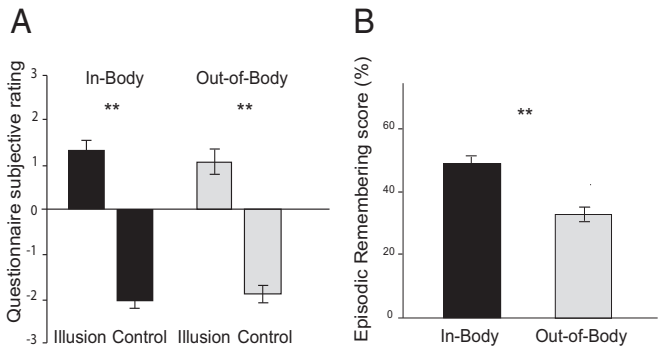

Fig. 2. Results of the first behavioral study (exp. 1). (*A*) Questionnaire data quantifying the in-body and out-of-body illusions during the encoding sessions (see *SI Results* for further details). (*B*) The results of episodic remembering assessed after 1 wk, using a standard life event episodic memory testing protocol (see Fig. S4 and *SI Results* for further details).

emotional engagement and self-evaluated performance for the "exam" (*SI Materials and Methods*). The experimenter then left the room, and the professor entered the room again for the next part of the exam. Four separate life events were enacted based on the semistructured scripts, and each life event was randomly assigned to the out-of-body condition or in-body condition. While developing the paradigm, we ensured that the emotional engagement and self-relevance of the life events were matched across the conditions (*SI Paradigm Development Exp. 1*). In total, each participant experienced two life events in the out-of-body condition and two life events in the in-body condition.

Out-of-Body–Induced Episodic Amnesia. In the first behavioral study, 32 healthy naïve volunteers experienced the life events as described above (exp. 1). The full-body illusion was rated as equally strong under both the in-body and out-of-body conditions (Fig. 2*A*), and the participants rated their performance (Fig. S2) and emotional engagement (Fig. S3) equally strongly across the conditions, ensuring a valid comparison of otherwise equivalent conditions (see *SI Results* for further details). One week later, the participants' episodic memory of these life events was examined using a structured interview, in which the examination topic was given as a cue for recall, and the participants had to recall each of the four life events as vividly as possible (*Materials and Methods*). The episodic quality of the recall experience was assessed (see *SI Materials and Methods*, for further details). The participants had significantly less episodic recall of life events encoded during the out-of-body condition compared with the in-body condition [exp. 1, encoding effect on episodic memory score, $F_{(32)} = 11.397$, $P = 0.002$; Fig. 2*B*; *SI Results*]. In line with our hypothesis of an impaired binding mechanism during encoding, the memory impairment included reduced spatial and temporal recall (Fig. S4).

In a second experiment, to exclude the possibility that differences in the visibility of the professor's face could be a confounding factor, we reproduced the out-of-body amnesia effect using a slight variation in the out-of-body condition. Now, the participant could always see the professor's face, instead of viewing him from the back as in the first experiment. We subjected a new group of 32 naïve participants to experiencing the out-of-body condition, using cameras placed to the side (30°) to obtain the full view of the professor from the front (and themselves from the side, Fig. 1*C*). Importantly, when memory was tested 1 wk later, we observed the same reduction in episodic retrieval of the life events encoded out-of-body compared with in-body [exp. 2, encoding effect on episodic memory score, $F_{(32)} = 4.811$, $P = 0.037$; Fig. S5 and *SI Results*].

Imaging Out-of-Body–Induced Amnesia. Next, we used fMRI to determine whether the out-of-body memory impairment was specifically associated with altered activation of the hippocampus. Previous fMRI studies have shown that the episodic recall of life events (episodic autobiographical memory) relies on a distributed set of brain regions that includes the hippocampus, the lateral temporal cortices, the temporo-parietal junction, the medial prefrontal cortex, the precuneus, and the retrosplenial cortex (28–30). The actual contents of the memory representation are believed to be stored in the cortex, with different cortical regions dynamically linked by the hippocampus during successful episodic encoding and retrieval (28, 29, 31–33). A recent neuroimaging study showed modulation of hippocampal activation by the level of rehearsal of a given autobiographical memory. Strong hippocampal activity was seen during initial autobiographical memory retrieval, but when individuals rehearsed the episode, there was progressive attenuation of hippocampal activity (34). Therefore, we predicted that the in-body condition would show a pattern of progressively decreasing activity as a function of repetition. Correspondingly, we predicted that the out-of-body–induced deficit in hippocampal activation would be most pronounced during early retrieval because an impaired binding mechanism during encoding should result in fragmented memories, which would be particularly difficult to retrieve fully and to relive vividly during the initial recall [in our factorial design, this prediction corresponded to a two-way interaction between the encoding condition (out-of-body vs. in-body) and the repetition (low, moderate, and high); see *SI Materials and Methods* and the following section for details].

Approximately 2 wk before the fMRI experiment (10–14 d; mean, 11.7 d), a new group of 21 naïve participants experienced the four life events, according to the procedures described for the first behavioral study (exp. 1). The blood oxygen level-dependent (BOLD) signal was registered with fMRI during repeated retrieval of the four life events (*Materials and Methods*). After each retrieval trial, the participants were asked to rate the vividness of the recollected memories, their difficulty in retrieving the memories, the emotional salience of the retrieval, and the adopted perspective during retrieval.

Before reporting the fMRI findings (see next paragraph), we analyzed the behavioral data from the scan sessions to provide complementary evidence for the hypothesis of hippocampus-based episodic memory impairment regarding events encoded out-of-body. Specifically, the vividness ratings of the recollected memories were relevant in this regard, as vividness ratings and episodic retrieval scores have been strongly correlated (35), and vividness ratings have been linked to activity in the hippocampo-cortical areas related to episodic memory (34, 36). Consistent with our neurocognitive predictions, the vividness ratings differed between the out-of-body and in-body conditions, depending on the number of repetitions [repetition by encoding interaction effect: $F_{(20,2)} = 9.753$; $P = 0.006$]. The first two retrieval trials of life events encoded in-body were rated significantly more vivid than the first two retrieval trials encoded out-of-body [$t_{(21)} = 3.866$, $P = 0.001$; Fig. S6*B*]. This difference was absent in subsequent trials (moderate numbers of retrieved episodes), and the opposite pattern emerged for multiple repeated retrieval trials (Fig. S7). Importantly, we observed no significant differences between the two conditions regarding the rated difficulty of retrieval, the emotional salience of retrieval, or the adopted perspective ($P > 0.05$), suggesting that the impairment was restricted to the vividness of the memories. In summary, these behavioral data from the fMRI experiment confirmed the results from the first two memory experiments (exps. 1 and 2) and provided independent behavioral support for our hypothesis regarding the out-of-body encoding effect on hippocampal activity during repeated retrieval (see above) (34).

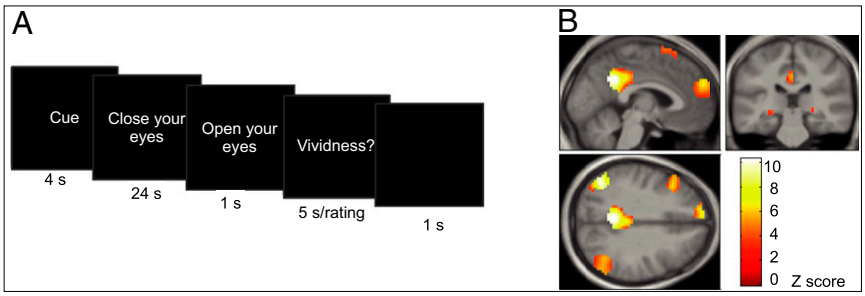

Fig. 3. Activation of the episodic retrieval network during the recall of the present life events. (*A*) Schematic illustration of the retrieval session during the fMRI paradigm. (*B*) The activation of the previously well-established network of episodic retrieval of life events when contrasting the retrieval conditions with the baseline imagery condition (main effect of retrieval) (all activations show $P < 0.05$, corrected; the scale denotes t values; the activations were superimposed on a mean T1-weighted structural scan in the MNI standard space generated from the structural scans of all participants, and masked with the search space of the episodic autobiographical network). The data indicate self-related medial cortical areas activated during both in-body– and out-of-body–encoded life event recall.

In the fMRI analyses, we first identified the areas that were more active during the retrieval of life events, compared with the baseline task (*SI Materials and Methods*). As expected, we observed increased activation of the bilateral retrosplenial cortex, the medial prefrontal cortex, the hippocampal region, the bilateral temporal pole, and the left angular gyrus across the two conditions (Fig. 3*B* and Table S1). This set of areas corresponded well with observations in previous neuroimaging studies (29, 32), thus validating the ecological aspect of the encoding session.

Next, we tested our main hypothesis of disturbed hippocampal activation when retrieving life events that had been encoded out-of-body (compared with in-body). In accordance with this hypothesis, the left posterior hippocampus was the only area showing the predicted pattern of activity [interaction between the encoding condition (out-of-body vs. in-body) and repetition (low, moderate, high); peak voxel in the Montreal Neurological Institute (MNI) coordinates: −27, −31, −11, $Z_{(21)} = 3.63$, $P = 0.019$; familywise error (FWE), corrected using small volume corrections on the left and right hippocampi; Fig. 4*A*]. For events encoded in-body, the left posterior hippocampus was strongly activated during the initial retrieval trials, but it showed progressively less engagement with further repetition (Fig. 4*B*), mimicking previous findings of a rehearsal effect (34). A qualitatively different pattern of activation was observed during repeated retrievals for out-of-body–encoded events (Fig. 4*B*), in which the left posterior hippocampus was not recruited during the initial retrieval trials but was instead recruited during later trials (only after many repetitions). Thus, the recall of events experienced out-of-body was not only associated with diminished hippocampal responses during the first recall, suggestive of specific episodic encoding impairments, but continued recall of these experiences resulted in a complete reversal of the pattern of activation (34) (see *SI Discussion*, for further information).

Moreover, we observed a correlation between the specific pattern of activation in the left hippocampus and the reported degree of out-of-body–induced memory impairment across individuals. The greater the participants reported a reduction in the vividness of the remembered events encoded out-of-body compared with in-body, the greater the reversal was of the normal pattern of hippocampal activation across retrieval trials (encoding by repetition effects; $P = 0.022$ after FWE correction for small volume correction on the left and right hippocampi; $R^2 = 0.458$; see Fig. 5 for details). Taken together, these imaging results associate out-of-body–induced episodic memory impairment with altered hippocampal recruitment.

Discussion

In this study, we used a multisensory full-body illusion in healthy individuals to simulate an out-of-body dissociative experience, during a realistic, real-life social event. This approach allowed us to test the hypothesis that episodic memory encoding of an event would require the perception of that event from within one's own body (first-person perspective). The experiments revealed two important findings. First, the behavioral results showed that episodic encoding of life events requires perceiving the world from the first-person perspective centered on one's real body, and violations of this basic condition produced impaired episodic recall, indicative of fragmented encoding. Second, the brain imaging data demonstrated that encoding events experienced out-of-body specifically impacts the activation of the left posterior hippocampus during retrieval, suggesting an impaired hippocampal binding mechanism during encoding (see below). These findings are fundamentally important, as they suggest a link between the ongoing perceptual experiences of the body and the world from the first-person perspective and the hippocampal episodic memory system. This empirical observation provides a basis for models of episodic memory (1, 2, 7, 8, 29, 31, 32, 34) and self-consciousness (10, 13, 14, 37), and it is a striking example of embodied cognition (38, 39), in which multisensory body self-perception directly influences a specific higher cognitive function, namely the episodic long-term memory system.

Under normal conditions, an individual experiences the world from the perspective of the physical body, and his/her center of

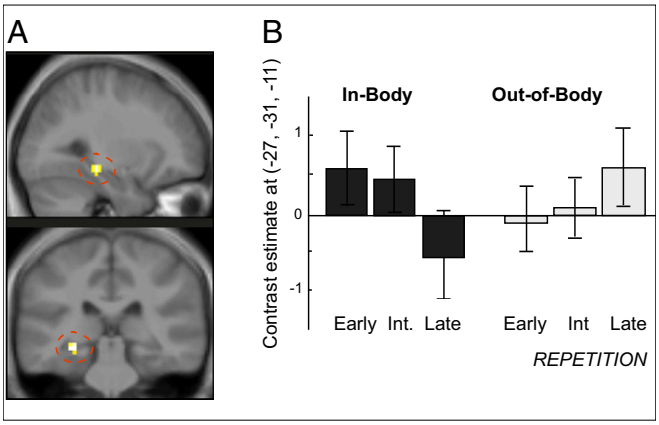

Fig. 4. The out-of-body experience specifically affected the activation of the posterior segment of the hippocampus. (*A*) Reduced activation of the left posterior hippocampus when retrieving life events encoded out-of-body compared with those encoded in-body, particularly during the early retrieval trials (interactions between condition and repetition). (*B*) The plots of the estimated BOLD effect size.

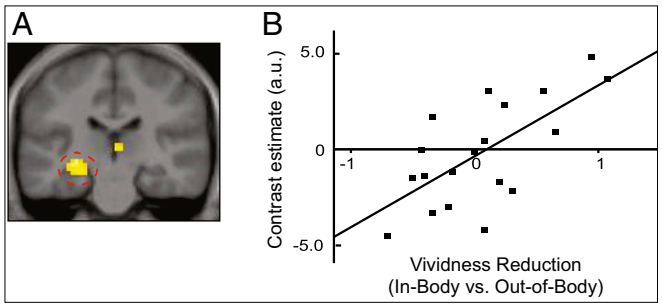

Fig. 5. Results of linear regression analysis of the fMRI data. (*A*) The results of the whole-brain linear regression model relating the effect size of the fMRI interaction term (between condition and repetition) to differences in vividness ratings between the out-of-body and in-body events. (*B*) The reduced vividness between out-of-body– and in-body–encoded events was linearly associated with the amplitude of the BOLD effect size in the left hippocampus.

awareness, or self, is located inside the physical body (12, 13, 40). This sense of owning a body in space defines the egocentric reference frames used to generate spatial representations of the external environment (41–43). In the present study, we used a perceptual illusion to influence and to relocate fully this basic sense of bodily self to a location outside the physical body. Thus, our results provide insights into the link between spatial body perception and the episodic memory system on a fundamental level. The experimental manipulation consisted of spatially and temporally correlated visual, auditory, and somatosensory signals (12, 27), which caused changes in the central perceptual construct of one's own body in space—a construct that is produced through the continuous integration of information from multimodal sensory inputs at the level of cortical multisensory association areas (13, 14).

The out-of-body dissociative experience impaired the episodic encoding process because the perceived and physical self-locations were in the distance, thus violating the default egocentric information processing among the various multisensory, emotional, social, and cognitive representations of the bodily self. The multisensory experience of one's own body is encoded in egocentric reference frames (hands, arm, head, and body-centered coordinates) in the premotor, posterior-parietal, and subcortical structures (13, 44, 45). Although less is known about the reference frames adopted for the emotional, social, and high-level cognitive representations of self (11, 46, 47), the out-of-body dissociative experience have impacted the integration of these processes during the self-relevant social interactions that constituted the present life events. Thus, we theorize that the out-of-body state interfered with the binding of information from multiple sensory and cognitive channels into coherent representations during encoding (4, 7, 17–19). (For further discussion of the hippocampus, body, and space, see *SI Discussion*.)

A number of cognitive, contextual, and emotional factors contribute to how well a particular episode is encoded and recollected (1, 48–51). In the present study, these factors were therefore carefully controlled. It has been well established that events that evoke strong emotions are remembered better than less emotional events (52) and that self-relevant events are remembered better than events that are less self-relevant. With this point in mind, we designed the current life events to evoke similar levels of modest emotions with equal self-relevance; this effect was further ensured by the randomization of events across conditions and participants (*SI Materials and Methods* and *Paradigm Development Exp. 1*). Importantly, we ensured that these factors were matched across in-body and out-of-body conditions to allow for the comparison of otherwise equivalent conditions (Figs. S2 and S3 and *SI Results*). The out-of-body condition was not more "distracting," and it did not affect general cognitive functions (*SI Results*) or performance on a verbal fluency task (*SI Paradigm Development Exp. 3* and Fig. S8) more than the in-body condition. Finally, it might be argued that the illusory out-of-body experience constituted a highly unusual experience; but "bizarre" events are remembered better than ordinary events (53) and we observed the opposite of a "bizarreness effect" in that the in-body–encoded events were remembered better.

Our study outlines a neuroscientific framework for understanding why patients who experience an out-of-body dissociative events often exhibit long-term memory problems [e.g., in post-traumatic stress disorder (25), borderline disorder (23), and schizophrenia (24)]. This research could be clinically significant, as dissociation, including out-of-body experiences, is a major vulnerability factor for psychopathology (22, 54). Given the apparent requirement of a natural first-person perspective between the body and the world for intact hippocampal memory function, a dissociative out-of-body experience during an acutely stressful event could, by itself, impair the encoding mechanism and produce fragmented, spatiotemporally disorganized memories. This potentially patho-neurocognitive mechanism could be the target of future research into treatment strategies for individuals suffering from dissociative experiences and memory problems in a wide range of psychiatric conditions and disorders.

Materials and Methods

Participants. In total, 129 participants were included in this study: 44 participants were included for the paradigm development experiments (Table S2); exps. 1 and 2 each included 32 healthy participants; for exp. 3, we recruited 21 healthy participants. All of the volunteers provided written informed consent before participation, and none of these individuals exhibited a history of psychiatric or neurological disorders. The Regional Ethical Review Board of Stockholm approved this study, and the experiments were conducted according to the principles expressed in the Declaration of Helsinki. For further details, see *SI Materials and Methods*.

Virtual-Reality Technology. During the encoding session, the participants were seated in a chair in a relaxed position and were instructed not to move. Each participant wore a pair of HMDs (Cybermind Visette Pro PAL; Cybermind Interactive; display resolution, 640 × 480 pixels; color displays) with a wide field of view (diagonal field of view, 71.5°). The HMDs were connected to two synchronized CCTV cameras (Protos IV; Vista) placed side by side (adjusted to match the distance between the eyes, 8–10 cm) and mounted on a tripod. Two pairs of cameras were mounted on tripods placed at two different locations in the room. The participants also wore a set of studio-quality earphones. The earphones were connected to a pair of microphones placed inside the ear canals of an advanced dummy head microphone, which provided a rich 3D sound space of the room from the perspective of the dummy head (KU 100 dummy head audio system; Neumann artificial head stereo microphone system). This advanced microphone was placed below the tripod with the mounted CCTV cameras. During the recall session, the participants were seated next to a table in a different testing room that did not include any of the furniture from the encoding sessions, and they did not wear the HMDs or the earphones (exp. 1, exp. 2); also for the fMRI experiment, they lay on the bore inside the MRI scanner (exp. 3). For further details, see *SI Materials and Methods*.

Memory Testing. Approximately 1 wk after the encoding session (see main text above), the participants' abilities to retrieve these events were examined using a structured interview, in which the participants had to retrieve each of the four events as vividly as possible, providing details of when and where the event occurred, what happened, and what they felt (55). A remember/know task followed. On the basis of these results, an "episodic remembering score" was computed, which reflected the episodic memory quality of the recall (see *SI Materials and Methods* for further details about the memory testing procedures and analysis).

fMRI. Functional imaging data were collected using a 3.0-T Siemens MRI scanner. The image volumes were preprocessed, spatially normalized to the standard MNI space, and analyzed with standard procedures, using Statistical Parametric Mapping software, version 8 (SPM8) (see *SI Materials and Methods*

for further details). Only activations that corresponded to $P < 0.05$ after correction for multiple comparisons in a random-effects analysis are reported. For further details, see *SI Materials and Methods*.

Supporting Information includes *SI Materials and Methods, SI Results, SI Discussion, SI Paradigm Development Experiments* (three experiments), Figs. S1–S9, Tables S1 and S2, and Movies S1–S3.

ACKNOWLEDGMENTS. We thank Chris Frith and Torkel Klingberg for their valuable comments on the manuscript, Alexander Skoglund for technical support (virtual-reality equipment), Peter Bergared (acting) and Victor Criado (play writing) for their help in setting up the life events play, and Andreas Kalckert, Björn van der Hoort, Christopher Berger, Giovanni Gentile, Laura Schmaltz, Valeria Petkova, and other laboratory members for their assistance with the out-of-body illusion induction and/or fMRI acquisition. This study was funded through grants from the European Research Council, the Swedish Foundation for Strategic Research, the Human Frontier Science Program, the Söderbergska Stiftelsen Foundation, the James S. McDonnell Foundation, and the Swedish Research Council. L.B. was supported by a postdoctoral fellowship from the Wennergren Foundation. L.N. was supported by a grant from the Knut and Alice Wallenberg Foundation, the Torsten and Ragnar Söderberg Foundation, and Umeå University's Strategic Neuroscience Program. L.N. and H.H.E. are members of the Strategic Research Program in Neuroscience in Sweden.

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Supporting Information

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SI Materials and Methods

Participants. In total, 129 participants were included in this study. The participants were all students recruited from universities in Stockholm. The participants were prescreened for DSM-IV Axis I disorders, using the Mini-International Neuropsychiatric Interview and the Beck Depression Inventory (BDI). The inclusion criteria were based on a BDI score of ≤8. None of the individuals exhibited a history of psychiatric or neurological disorders. The participants were all fluent English speakers.

For behavioral experiment (exp.) 1 and exp. 2, 32 naïve healthy volunteers were recruited (exp. 1: mean age ± SD, 26 ± 5 y; 13 women and 19 men; exp. 2: mean age ± SD, 27 ± 6 y; 16 women and 16 men). The same protocol was followed for both experiments.

For exp. 3, the functional magnetic resonance imaging (fMRI) experiment, an additional group of 21 naïve healthy volunteers was recruited (mean age ± SD, 26 ± 4 y; 11 men and 10 women).

The Regional Ethical Review Board of Stockholm approved this study, and the experiments were conducted according to the principles expressed in the Declaration of Helsinki. The participants were recruited at universities in Stockholm.

Basic Experimental Setup and Virtual-Reality Technology. The encoding of sessions with life events experienced in-body or out-of-body (see further details below) was conducted in a specially designed testing room (3.5 m × 6 m). We carefully designed the interior of the testing room to match the number and type of objects across life events (see further details below). A poster was changed for each life event, so a different poster was used for each event. The participants were briefly familiarized with the room and the objects within the room before the experiment began.

As indicated in the main text, two pairs of cameras were mounted on tripods placed in two different locations in the room. We controlled which pair of cameras fed video signals to the head-mounted displays (HMDs) worn by the participants. One set of cameras was placed behind and slightly above the participant's head, and the participant could see the room and the actor standing in front of him or her from a normal perspective, i.e., from the same perspective as if looking at the room directly without the HMDs (in-body condition; see Fig. 1*A* of the article). In exp. 1 and exp. 3, the other set of cameras was placed 2 m in front of the participants and was rotated 180° to face the participant directly (Fig. 1*B*; this paradigm was also used in paradigm development exps. 1–3; *SI Paradigm Development Experiments*). From this perspective, the participant's illusory body was placed behind the actor; he or she viewed the back of the actor talking to the participant, and the participant faced the cameras (with the HMDs; Fig. 1*B* of the main article). Thus, in both the in-body and out-of-body conditions, the participants viewed a face and a room interior, which we designed to match the number and type of objects visible. In exp. 2, the other set of cameras was placed 1 m to the right of the participant and was rotated 30° to gain the perspective of the participant from the side and the actor from the front. The illusory body location from the side facilitated the assessment of the out-of-body effect when viewing the full face of the actor (Fig. 1*C* in the main article).

The participants also wore a set of studio-quality earphones. The earphones were connected to a pair of microphones placed inside the ear canals of an advanced "dummy head microphone," which provided a rich 3D sound space of the room from the perspective of the dummy head (KU 100 dummy head audio system; Neumann artificial head stereo microphone system; Neumann GmbH). This advanced microphone was placed below the tripod with the mounted closed-circuit television cameras. With this arrangement, the participant could see and hear the room and the individuals within it from the two different locations, i.e., from "within the body" (in-body condition) and from "outside of the body" (out-of-body condition). The 3D sound from these perspectives facilitated the maintenance of the in-body and out-of-body illusions (see next paragraph). There were no noticeable delays in the video or auditory systems (delays of less than 25 ms).

Induction and Assessment of Out-of-Body and In-Body Illusions. ***Induction and maintenance of illusions.*** Before each life event encoding session started (see next section below), we elicited a multisensory illusion of being located in the place of the displaying cameras and sensing an "illusory body" at this location (1, 2). To this end, we delivered repetitive, synchronous visuotactile stimulation using two small plastic rods with a rhythm of 80 bpm for ∼70 s. One experimenter stood directly in front of the displaying cameras and moved a rod toward a point below the field of view of the cameras. When the rod reached this point, it corresponded visually to where the participant's chest would have been if he/she were sitting right behind the cameras. Simultaneously, synchronizing these touches as closely as possible, a second experimenter touched the participant's actual chest, which was out of view of the participant, at the corresponding location, following audio instructions presented in the earphones worn by the experimenter. Thus, the participant viewed the experimenter's arm approaching the cameras and then disappearing below the field of view; at this point, he or she felt a touch on his or her chest with a rod-like object. As in previous full-body illusion experiments (1–4), this type of synchronized visuotactile stimulation produced a multisensory illusion that the approaching rod was directly touching the participant's chest and that the participant's body was located directly behind and below the cameras, which was accompanied by the feeling of no longer self-identifying with the real physical body observed at a distance (1, 2, 5).

After the induction period with visuotactile stimulation, the illusory experience of self-location and body ownership was maintained with our audiovisual experimental setup (the technology was as described above; see further *Paradigm Development Exp. 2* below and Fig. S1). The spatially and temporally congruent visual (HMDs) and auditory information (earphones and dummy head microphone), from the perspective of the illusory location, facilitated the maintenance of the illusion in accordance with the spatial and temporal congruency principles of multisensory integration (6, 7). The illusion was not disrupted by social interaction and was maintained for the 5-min life events (Fig. S1 and *Paradigm Development Exp. 2*). We used identical procedures to induce the illusion in both conditions (in-body and out-of-body; see further below) throughout all of the experiments.

Assessment of illusions. For the main experiments (exps. 1–3), the strength of the illusory self-location and the illusory sense of body were registered at the very end of the encoding session (as described below), after all of the life events were experienced, to ensure that the participants were genuinely naïve to the illusion manipulation during the life events encoding. Thus, we repeated the induction of the out-of-body and in-body illusion conditions once more. Immediately after the 70 s of repeated visuotactile stimulation, the participants were asked to complete a questionnaire, in which they had to record six possible perceptual effects using a seven-point visual analog scale. Two of the questions

were designed to capture the experience of illusory self-location and ownership of the illusory body, whereas the other four questions served as controls for suggestibility and task compliance (1).

To analyze the strength of the illusory experiences statistically, we used a paired t test for the rating scores (i.e., the average score on the two illusion statements vs. the average score on the control statements). We also compared the level of the illusion strength between the conditions with a paired t test.

In paradigm development exp. 2, we registered the strength of the illusion, both immediately after the 70 s of visuotactile stimulation and after 5 min of social interaction without visuotactile stimulation. As described in detail below, the illusion was maintained at the end of the 5 min of social interaction (Fig. S1).

Encoding Sessions and Life Events (Exp. 1 and Exp. 2). ***Real-life events were created by "performance theater" with an actor.*** To create realistic, ecologically valid life events for encoding into long-term episodic memory, we worked with a professional actor to develop emotionally engaging, natural social interactions with a high degree of self-relevance. Actors are experts in producing systematic verbal material and social interactions in a believable and consistent manner, while respecting the contents of the scripts across multiple performances and also responding to the participants' behavior in a natural way.

With the assistance of the actor, we developed four separate episodes, which we also refer to as "life events" (for the preparation of these events, see *Paradigm Development Exp. 1*). The scripts for the episodes were based on a play written by Harold Pinter; they were made less emotionally intense and provocative and were adapted to a situation in which a professor is administering an oral examination to a student (the participants were all students at a major university in Stockholm, which enhanced the self-relevance of the script). Each episode took the form of performance theater; the student could orally interact with the "professor" and respond to his questions, as the professor examined the student's knowledge in specific areas.

In these four separate episodes, the professor evaluated four different areas of knowledge. These episodes corresponded to the four life events of the encoding session: an oral examination on geopolitics (life event 1); an oral examination on mechanics (life event 2); an oral examination on neuroscience (life event 3); and an oral examination on poetry (life event 4). These life events were mildly emotional (*Paradigm Development Exp. 1*), as the professor was sometimes eccentric, and the students wanted to perform well on the oral examinations. We also included information of a personal nature, such as information about a relationship with a close friend, in the scripts to enhance the self-relevance of the material. The actor (professor) followed the semistructured script that allowed for some improvisation, depending on the student's verbal responses, personal information, and knowledge (e.g., to enhance self-relevance, questions about the close friend and his/her relationship with the participant were incorporated into each episode).

Encoding session: step-by-step procedures. The participants were first required to read the written information about the encoding session, and they were then informed that the experiment tested knowledge under virtual-reality situations. That the professor was an actor was not explicitly mentioned to the participants, and the specific aims and hypotheses of the study were not revealed at this point. In addition, a document presenting information about the four topics that formed the basis of the knowledge evaluation was also provided to the participants. The participants were given 10 min to read this document before being led into the testing room, seated, and equipped with the HMDs and earphones.

After the illusion induction (see above), the professor entered the testing room and initiated the knowledge evaluation procedure (i.e., the "oral exam," as it was known to the participants, or the "life event-encoding sessions," which was the technical term used by the scientists). The actor playing the professor did not know which of the two pairs of cameras was actively connected to the participants' HMDs. Therefore, he did not know from which perspective the participants were experiencing the life events (i.e., the actor was blinded to the experimental conditions). Each life event had a mean duration of 5 min.

Before the four life events commenced, an initial "introductory event" was enacted. This event served several purposes. First, it provided the participants the opportunity to become used to the HMDs, as well as the setup in the testing room, and to become acquainted with the professor. Second, this event provided the actor with an opportunity to ask questions of a personal nature about the participant; this information was included in the subsequent scripted episodes to enhance the self-relevance of the material.

Each life event ended with the professor leaving the room and the experimenter entering the room. The experimenter asked questions about the participants' experiences of the oral examination (self-rating of the performance using a vertical scale from 0 to 100; and self-rating of the emotional level using a vertical scale from −100 to +100, with −100, very negative emotions; 0, no emotion; and +100, very positive emotions) to assess and enhance the active engagement of the participant in the oral exams in both conditions. To analyze the data, we used a paired t test (out-of-body vs. in-body) for the rated performance and emotion scores. Finally, after all of the life events had ended, the strength of the full-body illusion was tested in the out-of-body and in-body conditions, as described in the previous paragraph.

In summary, the encoding session consisted of the following: (*i*) an out-of-body or in-body induction, the introductory event, and the questionnaire rating emotion related to the introductory event; (*ii*) an out-of-body or in-body illusion induction, event 1, and the questionnaire ratings (performance and emotion) about event 1; (*iii*) an out-of-body or in-body induction, event 2, and the questionnaire ratings (performance and emotion) about event 2; (*iv*) an out-of-body or in-body induction, event 3, and the questionnaire ratings (performance and emotion) about event 3; (*v*) an out-of-body or in-body induction, event 4, and the questionnaire ratings (performance and emotion) about event 4; and (*vi*) an out-of-body or in-body induction and a questionnaire assessment of illusion strength. In total, the encoding session lasted ∼80 min.

Retrieval Session (Exp. 1 and Exp. 2). The retrieval session occurred 1 wk (8) after the life event-encoding sessions, to ensure long-term memory storage. The session took place in a different testing room from that used for the memory-encoding experiments. This testing room was a small soundproof psychophysics testing room without any of the furniture or virtual-reality equipment used in the life event-encoding sessions. The participant sat in front of a table with the experimenter. The four main events were assessed in randomized order. The average total duration of the retrieval session was 60 min.

Long-term episodic retrieval of life events was tested with a semistructured interview (9), based on a widely used memory task. This task assesses the episodic recall ability of specific life events. We adapted it to the requirements of the present experiment, which were to assess the episodic recall of the life events of the encoding session (see above).

The order of the life event recall was randomized. The participants were not informed or cued on the out-of-body or in-body conditions, and the experimenter was blinded to it. The participants were cued only with the topic of the oral examination (out of the four topics) and were asked to recall that life event as vividly as possible. After full retrieval of the life event, the participants were requested to provide a subjective report of their state of consciousness during that retrieval, with the assessment of the episodic recall on four main categories—"emotion," "what,"

"where," and "when"—using the remember/know (R/K) paradigm (see further details below).

According to Tulving's theory (1985), remembering and knowing are two different states of consciousness, which reflect autonoetic and noetic consciousness, respectively, i.e., episodic and semantic memory. The subjective phenomenal experience can be assessed via the R/K paradigm (10, 11), which requires the subjects to provide a "remember" (R) response if retrieval is accompanied by the recollection of specific experiences present at encoding or a "know" (K) response if retrieval is achieved without access to information from the initial encoding context. The participants could also indicate whether they had simply guessed the recalled event (11). Notably, the categories (10–12) were explained carefully to the participants until each concept used in this test was thoroughly understood, before starting the retrieval session. The task was first performed with a practice cue (the introductory event, from immediately before the actual life events commenced; see above) to ensure full understanding of the task.

Thus, after completing the initial free recall of a life event, the participants were instructed to select one of the three categories of "remember," "know," or "guess," with regard to the emotional, factual, spatial, and temporal content of the recalled event. In addition, a further procedure was performed to assess whether the subjects could justify each of their "R" judgments, proving that they had effectively "relived" the original event in their mind. Accordingly, for each R response provided for the four categories of information (emotion, what, where, and when), the participants had to add contextual details from the original life event if they did not provide them spontaneously.

The R score was defined as the number of remember responses divided by the number of remember or know responses (remember responses without the associated details were discarded from the analysis). We computed separate R scores for each domain of the episode, including the emotional R, the factual R, the spatial R, and the temporal R. We subsequently computed the episodic score, which corresponds to the global R score, defined as the averaged score of the four domain-specific R scores.

To test the hypothesis that episodic retrieval for the events encoded in the out-of-body condition would be lower than the in-body condition, we used a paired t test (out-of-body vs. in-body) for the global remember score (i.e., the average of all four remember scores: emotion, what, where, and when).

fMRI (Exp. 3). ***Overview of experimental procedures for exp. 3.*** The experiment consisted of three sessions: prescan encoding; the scan session; and the postscan interview. The interval between the prescan encoding and the scan session was 11.7 ± 2.7 d (median of 12) (8), and the postscan interview occurred directly after the scan.

Prescan encoding session of the life events. The prescan encoding session used the same protocol for the life events as the encoding session of exps. 1 and 2, with minor changes. Thus, ∼1 wk before the fMRI, all of the participants experienced the four life events of the professor testing their knowledge on the oral examination in our specially designed testing room and the in-body and out-of-body illusions (see above for the description of exps. 1 and 2). The small difference in procedures was that, after each life event, the participants were asked to contribute four cue words to identify each event clearly. These cue words would later be used in the fMRI experiment to indicate which event to retrieve. The average duration of the encoding phase was 80 min, which was the same as in exps. 1 and 2.

Prescan practice of the task. Before scanning, the participants were provided written instructions about the episodic memory retrieval task, and the experimenter verbally repeated these instructions before the scan. For the retrieval trials, the participants were instructed to reexperience the life event in question mentally, press the button once they had the memory in mind, and maintain this memory vividly until the questions about the retrieval trial were presented on the screen (13–16). For the object imagery baseline condition, the participants were instructed to imagine the object against a blank background (17–19), press the button once they had this image in their mind, and maintain this image vividly until the presentation of the test questions on the screen.

Before scanning, the participants performed a practice session outside of the scanner to ensure that they could perform the memory retrieval and imagery tasks as instructed. For this practice session, we used the introductory event and an event corresponding to the memory of how they found their way to the laboratory 1–2 wk earlier. The participants were encouraged to ask questions about the procedures and the memory retrieval task to ensure that they understood the task fully. If the participants were unsure about the task, the practice session was repeated. To ensure further that the participants would not forget the instructions, they were verbally repeated before each run during the fMRI experiment.

fMRI paradigm. During the brain scans, each subject lay comfortably in a supine position on the MRI table. The participants could see a screen through a mirror placed on top of the head coil. The visual material was projected onto the screen as white text on a black background. The participants were also equipped with a set of headphones. The stimuli corresponded to written and auditory instructions that were created and presented with the Presentation software package (Neurobehavioral Systems) using a PC laptop. The participants used a four-button pad to respond by pressing with their right index finger.

The participants had two tasks to perform in the scanner, both of which were practiced before the scanning commenced (see previous paragraph). In the "retrieval task," the participants had to retrieve and reexperience one of the four events from the life events encoding session (see above), with the life event nominated through cue words presented on the screen. The second task, which served as a baseline, was the "object" task, in which the participants were instructed to imagine each object on a blank background (four different objects, each assigned randomly as a baseline to each event).

Each retrieval trial included the following: (*i*) the cue presentation (the topic and the four cue words; these were presented for a period lasting 4 s); (*ii*) combined written and verbal instructions saying "eyes closed" (lasting 1 s); (*iii*) the retrieval task, lasting 24 s, during which the participants kept their eyes closed and indicated when they had retrieved the memory by pressing any key (13, 14); (*iv*) a combined written and verbal instruction saying "eyes open" (lasting 1 s); and (*v*) the visual presentation of the four questions, after which the subjects had to rate the vividness of the memories, the difficulty in retrieving them, the emotional content, and the visual perspective during retrieval (first- or third-person perspective) on a scale from 1 to 4 (the presentation and response to each question lasted 5 s). A 1-s period separated the trials (interstimuli interval) (Fig. 3*A*). No explicit information or instructions concerning the encoded condition (in-body or out-of-body) was provided to the participants; their task was simply to reexperience the events.

Each object imagery trial included the following: (*i*) the cue presentation (object plus four descriptive words, lasting 4 s); (*ii*) a combined written and verbal instruction saying "eyes closed" (lasting 1 s); (*iii*) the object imagery task (with eyes closed) lasting 24 s, with the participants pressing a key to indicate that they had evoked a vivid image in their "mind's eye"; (*iv*) a combined written and verbal instruction saying "eyes open" (lasting 1 s); and (*v*) a question about the vividness of the mental imagery with the participants rating this on a scale from 1 to 4 (lasting 5 s). A 1-s interstimulus interval separated the trials (Fig. 3*A*).

The scan session consisted of six functional runs, each lasting 348 s. Each run included two repetitions of the retrieval trial and the object imagery trial ("baseline task trial"). The retrieval trials

were classified into events encoded under the out-of-body or in-body conditions. The retrieval and object imagery trials were consistently presented in pairs (randomly starting with either the retrieval or the baseline imagery condition). In total, each run was composed of two out-of-body retrieval trials, two in-body retrieval trials, two baseline for the out-of-body trials (i.e., object imagery trials), and two baseline for the in-body trials (i.e., object imagery trials). The retrieval trials and object imagery were repeated six times in total, permitting the examination of the effect of repeated retrievals of the same life events (20).

Postscan interview. Following the scan session, a debriefing was performed to verify that the participants had followed the task instructions. For each life event, the cue words were presented to the participants, and they had to report verbally what and how well they had retrieved while placed in the scanner. This process allowed us to confirm the participants' compliance with the task.

fMRI imaging parameters. Six functional runs of 137 contiguous volumes were acquired on a 3-T TRIO 12-channel TIM system (Siemens Medical Solutions), with a 12-channel head coil, using a gradient echo T2-weighted echo-planar imaging (EPI) sequence, which was sensitive to a blood oxygen level-dependent (BOLD) contrast (41 axial slices, 2.54-s repetition time, 25-ms echo time, 2,230-Hz bandwidth, 90° flip angle, 64 × 64 matrix, 192 × 192-mm^2 field of view, and 3 × 3 × 3-mm^3 voxel size). The first two volumes of each run were discarded to obtain signal equilibrium. High-resolution, 3D T1-weighted images (3D fast gradient echo inversion recovery sequence, 400-ms inversion time, 2,300-ms repetition time, 4.18-ms echo time, 150-Hz bandwidth, 9° flip angle, 256 × 256 matrix, 220 × 220-mm field of view, and 1 × 1 × 1-mm^3 voxel size) were acquired for anatomical localization of the activation maps.

Statistical analysis of behavior data from the scanner. Because of the known pattern of repetition effects on the episodic retrieval of life events (20), we expected a diminishing vividness of recall for the in-body–encoded events, whereas we hypothesized that this pattern would be different when repetitively retrieving the out-of-body–encoded events (expected to be initially less vivid because of encoding deficits). To evaluate this hypothesis, we used repeated-measure ANOVA with the type of encoding (out-of-body vs. in-body) and the repetition (early, moderate, or late) as a two-level within-subject factor and the vividness score as the dependent variable.

Statistical analysis for fMRI. The fMRI data were analyzed using Statistical Parametric Mapping software, version 8 (SPM8) (www.fil.ion.ucl.ac.uk/spm/software/spm8). The EPI volumes were realigned to the first image, corrected for slice timing, coregistered with the high-resolution T1-weighted image, and normalized into the standard stereotactic space of the Montreal Neurological Institute (MNI). This normalization used the MNI template and the transformations computed during the segmentation of the high-resolution T1-weighted image. Finally, the normalized EPI volumes were smoothed using an isotropic Gaussian kernel filter with an 8-mm full width at half maximum.

For each subject, we computed a first-level individual statistical parametric map (SPM) using the general linear model. We modeled the access and elaboration periods with separate regressors; we defined the end of the access period and the start of the elaboration period on the basis of the participants' keypad responses to indicate that they had retrieved the memory and were vividly holding it in their minds. Similarly, the object imagery conditions were divided into an initial period before the key response and a period after the key response, when the participants were vividly holding the image in their minds.

Regressors of no interest were defined for the question and rating periods, as well as the instruction periods, to model these signal changes, thereby effectively eliminating these effects from the comparisons of interest. All of the regressors were further convolved with the canonical hemodynamic response function. In addition, the motion realignment parameters were included in the model to eliminate residual effects related to head movement artifacts. Finally, a high-pass filter was applied to discard slow fluctuations in the BOLD baseline due to physiological and scanner noise.

For each subject, we defined 12 contrast images that were used for the 2 × 2 × 3 factorial design in the second-level random-effects model. The retrieval conditions were first contrasted with their respective object imagery baseline, and the 2 × 2 × 3 factorial design was then defined by the encoding factors (out-of-body vs. in-body), according to the repetition (early, first two repetitions; intermediate, third and fourth repetitions; late, the fifth and sixth repetitions) and the phase of retrieval (access vs. elaboration). Importantly, the literature has shown that the hippocampus is most active during the "access phase" of episodic autobiographical retrieval (14, 16), which corresponds to the period when the memory is constructed for the reexperience. Therefore, we focused our analysis on the predicted effects during the access phases, although we fully modeled both the access and elaboration phases in our paradigm (we used this information in the post hoc analysis mentioned in *SI Discussion*).

To test our prediction that the hippocampus would show decreasing activity with repetition for the in-body condition, whereas the out-of-body condition would show a deficit in early recall due to fragmented encoding, we focused on the access periods and inspected the 2 × 3 interaction between perspective (out-of-body vs. in-body) and repetition (early vs. intermediate vs. late). As described in *Results*, the data revealed significant activation of the left posterior hippocampus. The same pattern of activation was observed in the left posterior hippocampus during both the access and elaboration periods of the retrievals. There was no three-way interaction [perspective by repetition by phase (access vs. elaboration)] in the hippocampus.

The search space used for the correction of multiple comparisons comprised a large set of clusters corresponding to the episodic autobiographical network (21). All of the statistical images were first thresholded using an uncorrected voxelwise threshold of $P < 0.001$ to generate activation maps (22). We then corrected for multiple comparisons using the familywise error test. For voxels within the episodic autobiographical network region of interest, we corrected for the number of voxels within this region (which consisted of a set of large clusters). We also applied small volume corrections to the left and right hippocampi, and we report activations corresponding to $P < 0.05$ being corrected, in line with our a priori hypothesis regarding this structure (see main text).

Regression analysis. To identify a systematic relationship between the vividness reduction of the retrieved out-of-body–encoded memories and the BOLD signal, we used a second-level random-effect linear regression analysis (Fig. 5). Thus, for each participant, we first computed a contrast image corresponding to the interaction term (between the factors of perspective and repetition) that revealed the key activation of the hippocampus in the main analysis (*Results*). Subsequently, we computed the difference in the vividness rating between the retrieved out-of-body– and in-body–encoded events for each participant, and we defined a regression model with the reduction in vividness as a covariate and the contrast images from the BOLD interaction effect [the 2 × 3 interaction between perspective (out-of-body vs. in-body) and repetition (early vs. intermediate vs. late), as described above]. We searched for areas showing significant linear relationships throughout the whole brain and corrected for multiple comparisons within the search space of the episodic autobiographical network region of interest, in accordance with previous meta-analyses (21), using a small volume correction in the left and right hippocampi.

SI Results

Specificity of the Out-of-Body Effects on Episodic Memory (Exp. 1 and Exp. 2). Further analyses of the behavioral data assessed the effects of out-of-body manipulation on other cognitive functions than episodic long-term memory. First, the oral examination constituted a challenging cognitive task that involved the evaluation of complex factual knowledge; thus, if the out-of-body illusion affected general cognition, then the examination would have been more difficult for the participants to perform. We therefore analyzed how well the participants rated their performance on the oral exam. We observed that the ratings were comparable under the out-of-body and in-body conditions [Fig. S2, no difference in performance scales; exp. 1, $t_{(32)} = 0.579$, $P = 0.567$; and exp. 2, $t_{(32)} = 1.03$, $P = 0.31$]. These findings are consistent with the notion that experimental manipulation does not interfere with all high-level, demanding cognitive functions and that the overall cognitive performance was matched under both the in-body and out-of-body conditions. For further corroborative tests of this conclusion, see the results from paradigm development exp. 3 below.

Matched Full-Body Illusion Strength Across the In-Body and Out-of-Body Conditions (Exps. 1, 2, and 3). In the encoding session, after the four life events had been experienced, the participants were asked to rate the strength of the full-body illusion by completing a questionnaire concerning their illusory self-location and illusory sense of owning a body [adopted from Ehrsson (1)]. The illusion was strong in both perspectives in all of the experiments [exp. 1, in-body $t_{(28)} = 10.71$, $P < 0.001$; out-of-body $t_{(28)} = 9.67$, $P < 0.001$; exp. 2, in-body $t_{(32)} = 13.77$, $P < 0.001$; out-of-body $t_{(32)} = 10.64$, $P < 0.001$; exp. 3, in-body $t_{(21)} = 6.83$, $P < 0.001$; out-of-body $t_{(21)} = 5.89$, $P < 0.001$]. Importantly, there was no significant difference in the illusion strength between the two conditions, which therefore ensured the comparison of otherwise equivalent conditions for the episodic retrieval assessment results [exp. 1: $n = 28$; illusion strength difference, $t_{(28)} = -0.527$; $P = 0.602$; exp. 2: $n = 32$; illusion strength difference, $t_{(32)} = 0.883$, $P = 0.386$; exp. 3: $n = 21$; illusion strength difference, $t_{(21)} = -0.683$, $P = 0.501$]. For further information about the matched illusion strength across the conditions, see the results below from paradigm development exp. 2.

Retrieval Sessions (Exp. 1 and Exp. 2): Results from Individual Categories. The global episodic score encompasses the emotional, factual, spatial, and temporal aspects of the memories. The effect observed on the global score was mostly driven by the spatial, temporal, and emotional aspects of the memories in exp. 1 [encoding effect on the spatial episodic score, $t_{(32)} = 2.49$, $P = 0.018$; encoding effect on the temporal episodic score, $t_{(32)} = 3.74$, $P = 0.001$; encoding effect on the emotional episodic score, $t_{(32)} = 2.041$, $P = 0.05$; Fig. S4] and by spatial and temporal aspects in exp. 2 [encoding effect on the spatial episodic score, $t_{(32)} = 2.62$, $P = 0.014$; encoding effect on the temporal episodic score, $t_{(32)} = 2.90$, $P = 0.007$].

SI Discussion

The Present Results and Earlier Knowledge About the Hippocampus, Body, and Space. That the multisensory experience of self must be centered on the physical body for normal hippocampal episodic encoding is consistent with the established roles of the hippocampus in spatial navigation (23) and spatial representation (24–26). One common denominator in episodic memory and spatial navigation is the formation of a multisensory representation of the physical self with regard to the local surroundings, as the individual navigates through a complex environment or encodes the "where," "when," and "what" of a particular moment. Interestingly, neurophysiological experiments in rats have suggested that the formation of stable representations of the environment requires a directly embodied experience within a space (25), which is in general agreement with our findings. Future experiments in rodents, using virtual-reality technology (27, 28) and multisensory stimulation protocols, could presumably examine the mechanisms that underlie the link between the central construct of the bodily self and memory encoding at the level of single neurons. The sense of being located within the body and experiencing the world from this perspective could therefore constitute a basic prerequisite condition for the functioning of the hippocampo-cortical system.

Qualitatively Different Time Course of Activation During the Repeated Retrieval of Out-of-Body–Encoded Life Events. Why did the hippocampus show a qualitatively different time course of activation during the repeated retrieval of out-of-body–encoded events, compared with the normal pattern that emerged when recollecting events encoded in-body? For the early retrieval trials, the hippocampus showed no differential activity compared with the baseline task, and the memories were not rated as vivid, suggesting a fundamental impairment of the encoding and storing of the memories that translated into weak and non-significant recruitment of the hippocampus at retrieval. Subsequently, with repetition, a gradual increase in hippocampal activity was observed, suggesting the creation of new associations between spatially and temporally disorganized memory fragments of semantic knowledge (29). Thus, one would expect to observe the engagement of cortical regions associated with semantic processing, such as the middle temporal gyrus or the temporal pole (30), with events preceding hippocampal activation during repeated retrieval attempts. We searched for such activity over the entire episodic autobiographical memory network using a post hoc approach, and we observed a significant activation of the left middle temporal gyrus [peak voxel in MNI coordinates: −48, −1, −17; $F_{(21)} = 9.86$; $Z = 3.79$; $P < 0.001$, uncorrected; Fig. S9], which preceded hippocampal activation in a systematic manner (see the BOLD plots in Fig. S9 and Fig. 4*B*). Given that the left middle temporal gyrus and the left medial temporal complex are anatomically connected (31), one speculative interpretation is that the semantic information from the left middle temporal gyrus was used in the left hippocampus to create new associations, using the original unbound memory fragments.

SI Paradigm Development Experiments

Paradigm Development Exp. 1. To select the four emotionally mild and matched life events used in the main experiments (exps. 1–3), we recruited 10 healthy naive volunteers (mean age ± SD, 29 ± 8 y; five women and five men). The participants experienced nine initial scripted life events that consisted of a controlled social interaction with the professor. After each life event, the participants had to rate the level of emotions associated with the event on a vertical visual analog scale, from −100 (extremely negative) to +100 (extremely positive), with 0 indicating no emotion. The four most emotional life events were selected for the encoding sessions for exps. 1, 2, and 3. The mean emotional rating of the four selected episodes was −17.5 (±6.7), corresponding to a mildly negative emotional response. Thus, the selected life events had a moderate emotional level to ensure episodic long-term memory encoding.

Paradigm Development Exp. 2. To validate the maintenance of the full-body illusions in our setup with congruent 3D audio and 3D visual feedback over the 5-min-long life events involving a social interaction, we recruited 20 participants (mean age ± SD, 24 ± 4.7 y; 10 women and 10 men). We set the experimental paradigm with the out-of-body and in-body conditions exactly as described in the main text, and we administered the illusion questionnaire directly after each 5-min life event (visual-touch induction followed by audiovisual input during life event).

The experimenter was placed in front of the real body of the participants at a location that corresponded to the location where the actor was standing in main exps. 1 and 3. The experimenter conversed with the participant following a version of the script in which the participant had to answer questions on the texts used in the original scripts. Two life events were randomly assigned to the out-of-body condition, and two life events were randomly assigned to the in-body condition for each participant. At the end of each 5-min episode, we administered the illusion questionnaire. After the four life events session, an illusion induction–questionnaire procedure that was identical to the main experiments occurred, that is, we induced the illusion by delivering the synchronized dynamic visuotactile stimulation for 70 s.

Because the data did not follow a normal distribution in this sample, to assess the difference in the strength of the illusory experiences between conditions (questionnaire results after each life event: out-of-body vs. in-body; out-of-body after life-events vs. out-of-body after full session; in-body after life-events vs. in-body after full session) in the statistical analyses, we used Wilcoxon's test for paired samples. The results are presented in Fig. S1; there were no significant differences in illusion strength between the conditions ($P > 0.05$).

Paradigm Development Exp. 3. To address the concern that out-of-body manipulation might not only affect the long-term episodic memory system but also general cognition, we assessed the effects of the out-of-body conditions compared with in-body illusion conditions using a word fluency task, which probed frontotemporal semantic memory and executive functions (32), in an additional group of 14 naïve healthy volunteers (mean age ± SD, 30 ± 4.6 y; 4 women and 10 men). After the illusion induction (as in exp. 1), the experimenter sat in front of the participant's real body and administered the fluency task (letter-related word fluency, followed by semantic category fluency). After testing the performance on the fluency task under both the out-of-body and in-body conditions, we assessed the strength of the perceptual illusion as in exp. 1 and exp. 2 (see main text and above).

As the data did not follow a normal distribution in this sample, for the statistical analysis, we used Wilcoxon's test for paired samples (out-of-body vs. in-body), with the letter fluency score (i.e., the average of two letter-related fluency tasks) and the semantic fluency score. To confirm equally strong illusions across the two conditions (Fig. S8), we used Wilcoxon's test for paired samples with the rating scores (i.e., the average score on the two illusion statements vs. the average score on the control statements).

The results showed that, compared with the in-body condition, the out-of-body illusion did not produce a fluency deficit [verbal fluency; Fig. S8, out-of-body: 12.1 (±2.9) (mean ± SD); in-body: 12.2 (±2.6), $t_{(14)} = 0.111$, $P = 0.913$; for the category fluency: out-of-body: 22.2 (±11.2); in-body: 23.5 (±8.7); category fluency, $t_{(14)} = 0.306$, $P = 0.764$], with performance levels in the normal ranges for both conditions (33). These findings are consistent with the notion that experimental manipulation does not interfere with all high-level, demanding cognitive functions or with declarative memory per se, but it more specifically interferes with the hippocampal episodic memory system.

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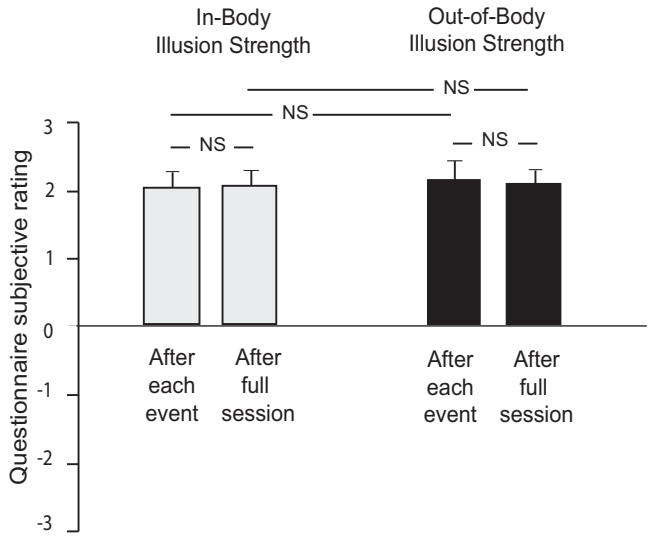


Fig. S1. Results of paradigm development exp. 2. Questionnaire data quantifying the in-body and out-of-body illusion strength after each 5-min social interaction and directly after a period of 70 s of visuotactile stimulation (as in main exps. 1–3). The illusion was equally strong in all cases.

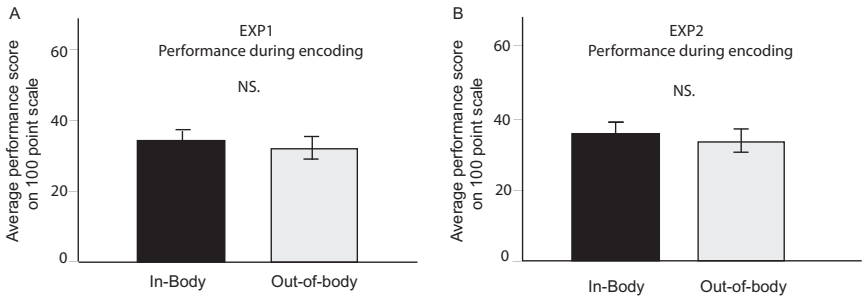


Fig. S2. Performance ratings during encoding throughout exp. 1 and exp. 2. (*A*) Performance ratings for the in-body and out-of-body conditions during the encoding sessions of exp. 1. (*B*) Performance ratings for the in-body and out-of-body conditions during the encoding sessions of exp. 2.

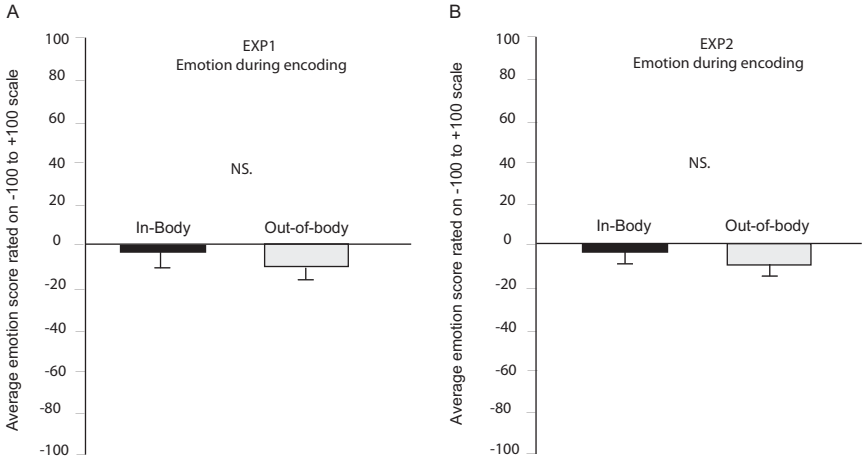


Fig. S3. Emotion ratings during encoding throughout exp. 1 and exp. 2. (*A*) Rating emotion for the in-body and out-of-body conditions during the encoding sessions of exp. 1. (*B*) Rating emotion for the in-body and out-of-body conditions during the encoding sessions of exp. 2.

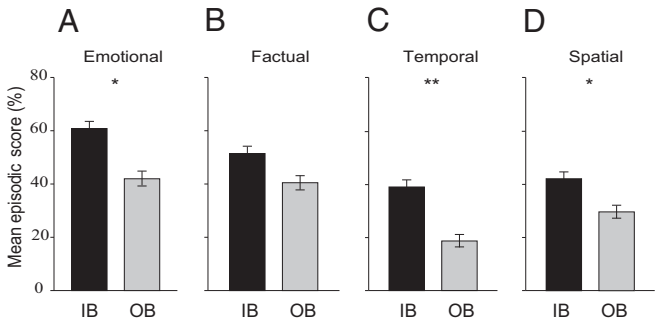


Fig. S4. Detailed results of the first behavioral study (exp. 1). Episodic scores for (*A*) the emotional aspect, (*B*) the factual aspect, (*C*) the temporal aspect, and (*D*) the spatial aspect of the event. Separate ANOVA analyses, with the memory scores using the four aspects of memory as the dependent variables, revealed a significant encoding effect for emotions ($F = 4.166$, df = 31, $P = 0.05$), spatial aspect ($F = 6.2$, df = 31, $P = 0.018$), and temporal aspect ($F = 13.971$, df = 31, $P = 0.001$). The effects on the factual aspect did not meet our criteria for significance ($F = 2.438$, df = 31, $P > 0.05$). As shown in Fig. 1*B*, when these four aspects were combined to generate a global retrieval score, the effect was significant ($F = 11.397$, df = 31, $P = 0.002$).

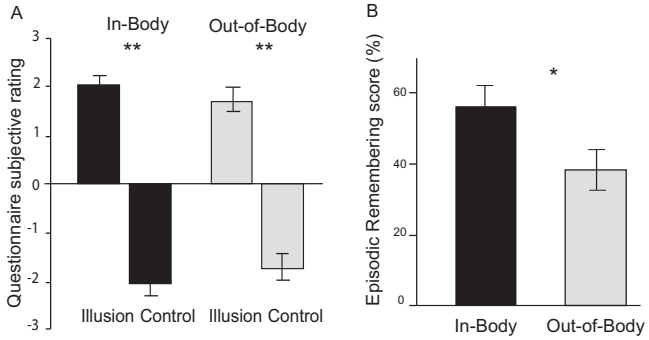


Fig. S5. Results of the second behavioral study (exp. 2). (*A*) Questionnaire data quantifying the in-body and out-of-body illusions during the encoding sessions. (*B*) The results of episodic remembering assessed 1 wk later, using a standard episodic memory testing protocol.

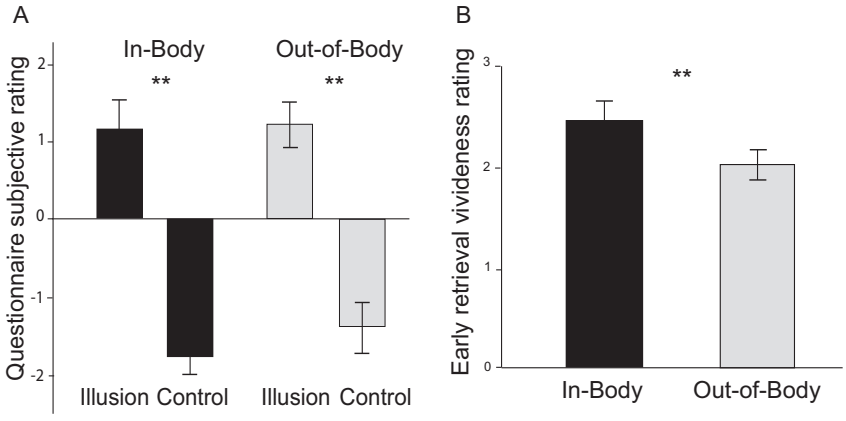


Fig. S6. Behavioral results of exp. 3. (*A*) Questionnaire data quantifying the in-body and out-of-body illusions during the encoding sessions. (*B*) Result of the vividness of early retrieval in the scanner.

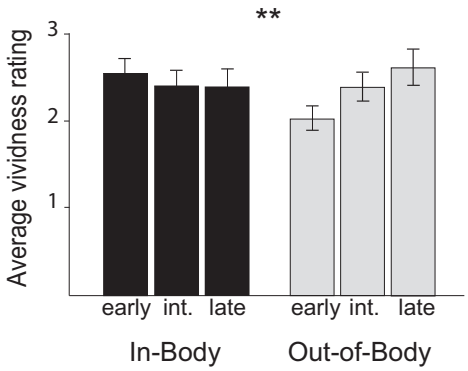


Fig. S7. Behavioral results obtained from the fMRI experiment. Results of the vividness rating acquired during the fMRI scans confirmed an episodic memory impairment effect for life events encoded out-of-body. The vividness rating was low for the initial recall of out-of-body life events, whereas an increase emerged with repetition, suggesting reencodings of the out-of-body life events with repeated retrievals.

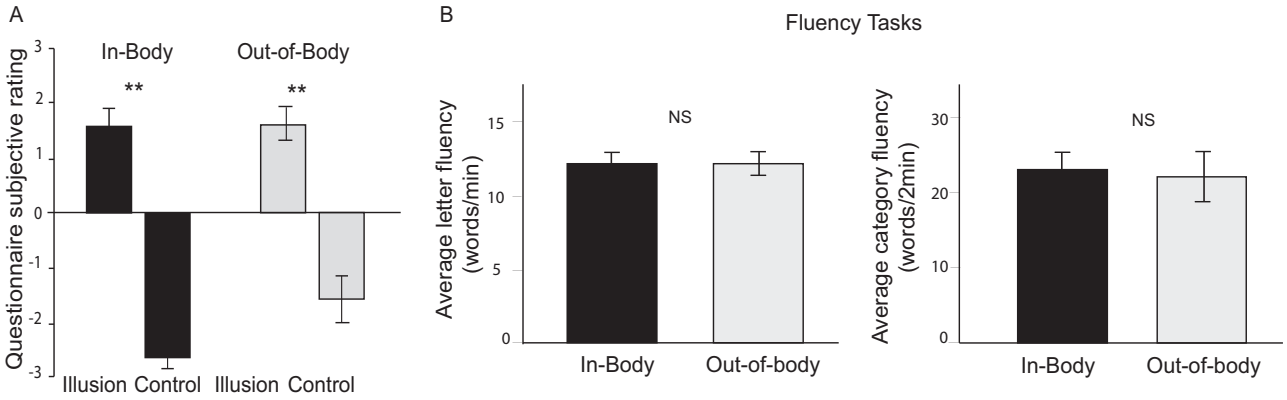


Fig. S8. Results of paradigm development exp. 3. (*A*) Questionnaire data quantifying the in-body and out-of-body illusions during the fluency task. (*B*) Results of the letter and semantic fluency tasks.

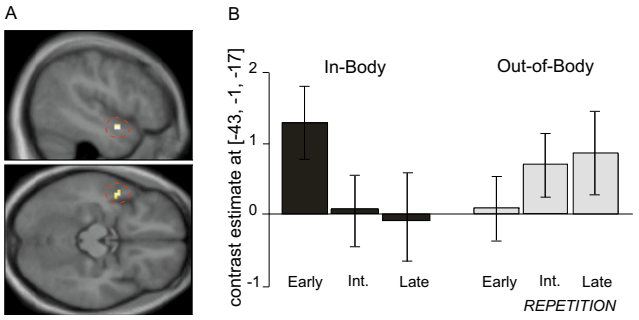


Fig. S9. Supplementary fMRI results of exp. 3. (*A*) Activation in the left temporal pole. The activation (-48 −1 −17; 8 voxels; $F = 9.86$; $Z = 3.79$; $P < 0.001$, uncorrected) was observed when inspecting the three-way interaction among perspective, repetition, and phase. (*B*) Strong activation was present with moderate repetition during the access phase of the out-of-body–encoded events, which occurred earlier than the activation of the posterior hippocampus (compared with the BOLD plots shown in Fig. 4*B*).

Table S1. Table showing the anatomical regions and the corresponding brain activation for the Retrieval vs. Control contrast and the Encoding by Repetition interaction effect within the episodic autobiographical network [false discovery rate (FDR) corrected]

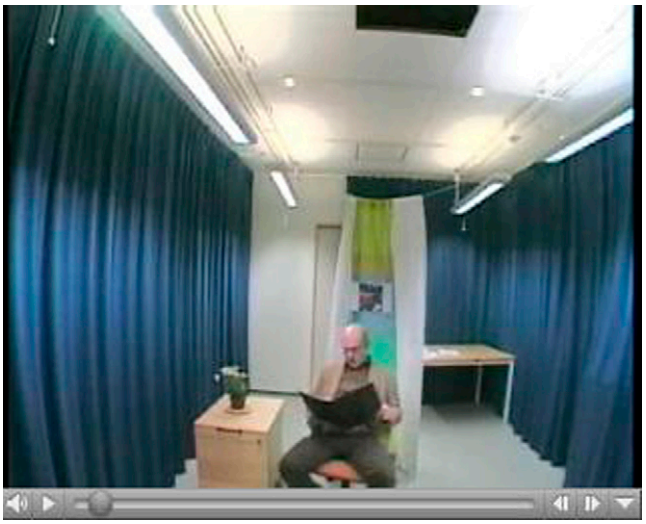
Anatomical region	Peak *p* (FDR corrected)	Peak *T*	Peak *Z*	MNI (*x*, *y*, *z*)
Retrieval vs. Control				
Temporal cortex				
L Hippocampus	0.016*	4.45	4.36	−24 −31 −2
R Hippocampus	0.048	4.27	4.19	24 −28 −2
L Middle temporal gyrus	<0.001	7.41	7.02	−57 −40 −2
L Middle temporal gyrus	<0.001	7.40	7.02	−54 −28 −5
R Middle temporal gyrus	<0.001	6.25	6.01	54 −10 −14
R Middle temporal gyrus	<0.001	5.54	5.37	57 −31 −2
Parietal cortex				
Precuneus	<0.001	11.59	Inf	−6 −64 31
Retrosplenial	<0.001	10.98	Inf	−3 −46 31
L Supramarginal gyrus	<0.001	10.41	Inf	−51 −61 31
L Supramarginal gyrus	<0.001	8.54	Inf	−39 −70 43
R Supramarginal gyrus	<0.001	8.25	7.73	42 −70 46
R Supramarginal gyrus	<0.001	5.93	5.72	60 −58 28
R Supramarginal gyrus	<0.001	5.83	5.63	51 −52 28
Frontal cortex				
L Superior frontal gyrus	<0.001	8.08	7.59	−39 14 55
R Middle frontal gyrus	0.034	4.38	4.29	42 11 55
R Middle frontal gyrus	0.034	4.38	4.29	57 26 25
Occipital cortex				
L Superior occipital gyrus	<0.001	9.24	Inf	−21 −94 1
Effect of Encoding by Repetition		Peak *F*	Peak equiv *Z*	
L Hippocampus (posterior)	0.019*	9.20	3.63	−27 −31 −11

L, left; R, right; Inf, infinite.
*Small volume correction on the left and right hippocampi: familywise error corrected.

Table S2. Overview of the experiments

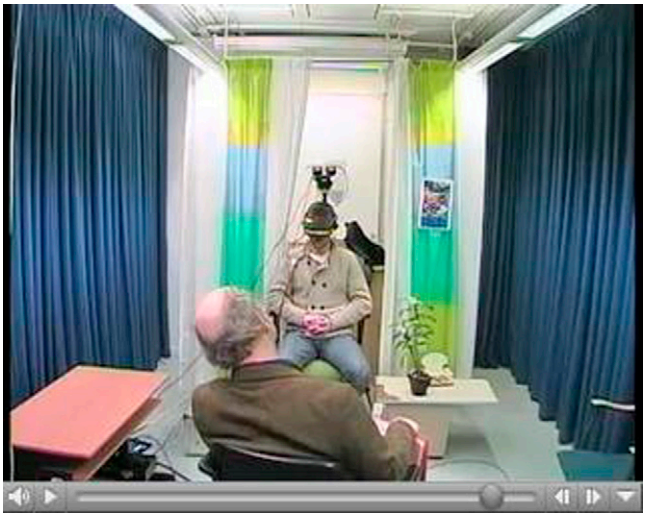
Experiment	Aim	Method	No. participants
Exp. 1	Test the main hypothesis behaviorally	In-body/out-of-body (180°) encoding in room 1; retrieval in room 2	32
Exp. 2	Retest the main hypothesis with face visibility	In-body/out-of-body (30°) encoding in room 1; retrieval in room 2	32
Exp. 3	Test the main hypothesis using fMRI	In-body/out-of-body (180°) encoding in room 1; retrieval in MRI scanner	21
Paradigm development exp. 1	Select four relevant life events	Selection of four life events of nine	10
Paradigm development exp. 2	Test the maintenance of out-of-body or in-body illusions after 5 min of the life event	In-body/out-of-body (180°) encoding in room 1: visual-touch induction, followed by audiovisual synchronous input during life event	20
Paradigm development exp. 3	Control for out-of-body effects on general cognitive tasks	In-body/out-of-body (180°) fluency task in room 1	14

This research included 129 participants in three main experiments and three paradigm development experiments. Note: Room 1 refers to the specially designed large testing room used for the enactment of the life events (with the actor). Room 2 refers to the traditional soundproof testing room used for the memory testing.



Movie S1. Small extract of the raw movie of the in-body condition.

Movie S1



Movie S2. Small extract of the raw movie of the out-of-body condition (180°).

Movie S2

Movie S3. Small extract of the raw movie of the out-of-body condition (30°).

Movie S3