Out-of-body–induced hippocampal amnesia

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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.

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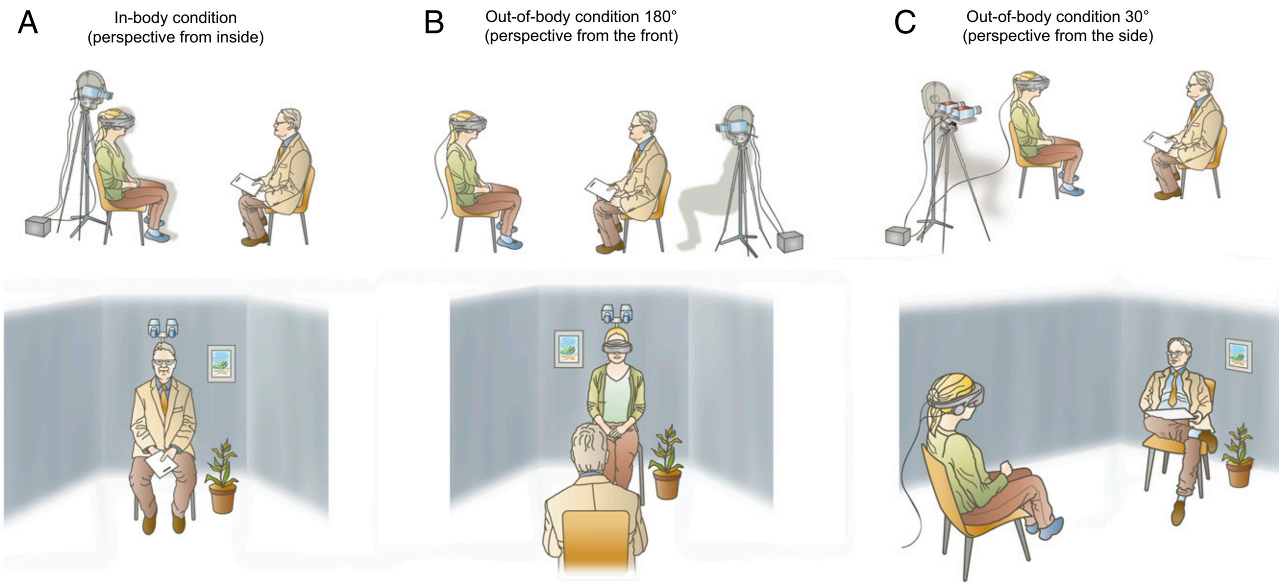

Fig. 1. Schematic representation of the experimental setup used during life event encoding. Manipulation of the experienced self-location (shaded figure) relative to the real body (filled figure with HMDs), in three experimental conditions during a social interaction with a professor (an actor; filled 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

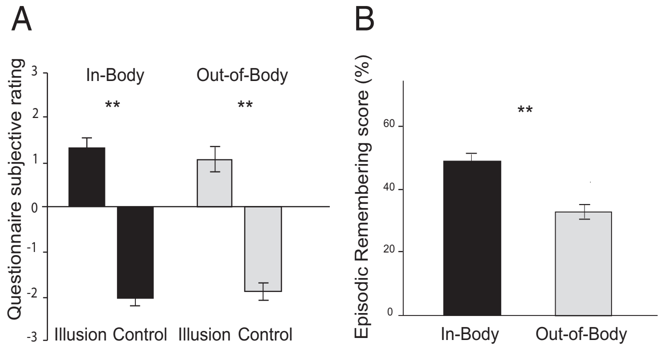

Fig. 2. Results of the first behavioral study (exp. 1). (*A*) Questionnaire data quantifying the in-body and out-of-body illusions during the encoding sessions (see *SI Results* for further details). (*B*) The results of episodic remembering assessed after 1 wk, using a standard life event episodic memory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

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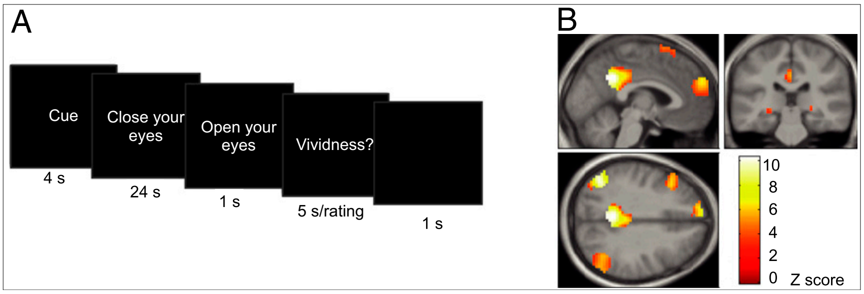

Fig. 3. Activation of the episodic retrieval network during the recall of the present life events. (*A*) Schematic illustration of the retrieval session during the fMRI paradigm. (*B*) The activation of the previously well-established network of episodic retrieval of life events when contrasting the 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

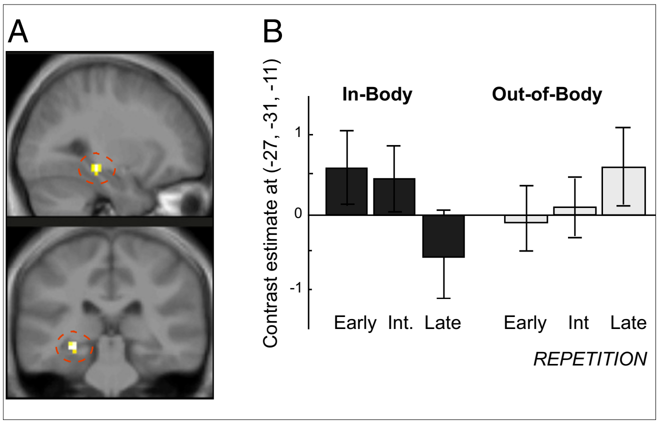

Fig. 4. The out-of-body experience specifically affected the activation of the posterior segment of the hippocampus. (*A*) Reduced activation of the left posterior hippocampus when retrieving life events encoded out-of-body compared with those encoded in-body, particularly during the early retrieval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

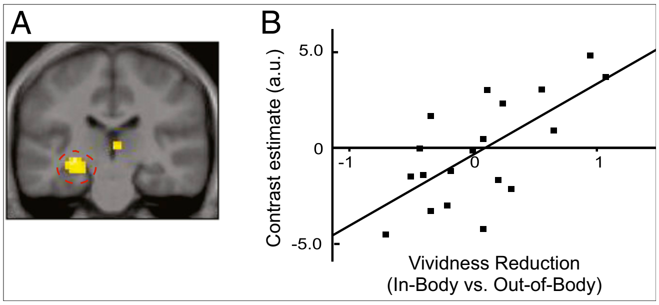

Fig. 5. Results of linear regression analysis of the fMRI data. (*A*) The results of the whole-brain linear regression model relating the effect size of the fMRI interaction term (between condition and repetition) to differences in vividness ratings between the out-of-body and in-body events. (*B*) The 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 posttraumatic 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.

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1. Tulving E (1983) *Elements of Episodic Memory* (Clarendon, Oxford).
2. Squire LR, Zola-Morgan S (1991) The medial temporal lobe memory system. *Science* 253(5026):1380–1386.
3. Cohen NJ, Eichenbaum H (1995) *Memory, Amnesia, and the Hippocampal System* (MIT, Cambridge, MA).
4. Nyberg L, McIntosh AR, Houle S, Nilsson LG, Tulving E (1996) Activation of medial temporal structures during episodic memory retrieval. *Nature* 380(6576):715–717.
5. Squire LR, Zola SM (1996) Structure and function of declarative and nondeclarative memory systems. *Proc Natl Acad Sci USA* 93(24):13515–13522.
6. Nyberg L, et al. (1996) General and specific brain regions involved in encoding and retrieval of events: What, where, and when. *Proc Natl Acad Sci USA* 93(20):11280–11285.
7. Eichenbaum H (2000) A cortical-hippocampal system for declarative memory. *Nat Rev Neurosci* 1(1):41–50.
8. Nyberg L, Habib R, McIntosh AR, Tulving E (2000) Reactivation of encoding-related brain activity during memory retrieval. *Proc Natl Acad Sci USA* 97(20):11120–11124.
9. Conway MA, Pleydell-Pearce CW (2000) The construction of autobiographical memories in the self-memory system. *Psychol Rev* 107(2):261–288.
10. Schacter DL, Chiao JY, Mitchell JP (2003) The seven sins of memory: Implications for self. *Ann N Y Acad Sci* 1001:226–239.
11. Buckner RL, Carroll DC (2007) Self-projection and the brain. *Trends Cogn Sci* 11(2):49–57.
12. Ehrsson HH (2007) The experimental induction of out-of-body experiences. *Science* 317(5841):1048.
13. Petkova VI, et al. (2011) From part- to whole-body ownership in the multisensory brain. *Curr Biol* 21(13):1118–1122.
14. Blanke O (2012) Multisensory brain mechanisms of bodily self-consciousness. *Nat Rev Neurosci* 13(8):556–571.
15. James W, James H (1911) *Memories and Studies* (Longmans, New York).
16. Gallagher S (2011) The self in the Cartesian brain. *Ann N Y Acad Sci* 1234:100–103.
17. Zeineh MM, Engel SA, Thompson PM, Bookheimer SY (2003) Dynamics of the hippocampus during encoding and retrieval of face-name pairs. *Science* 299(5606):577–580.
18. Rudner M, Fransson P, Ingvar M, Nyberg L, Rönnberg J (2007) Neural representation of binding lexical signs and words in the episodic buffer of working memory. *Neuropsychologia* 45(10):2258–2276.
19. Andersen P, Morris R, Amaral D, Bliss T, O'Keefe J (2007) *The Hippocampus Book* (Oxford University Press, Oxford).
20. Vargha-Khadem F, et al. (1997) Differential effects of early hippocampal pathology on episodic and semantic memory. *Science* 277(5324):376–380.
21. Conway MA (2009) Episodic memories. *Neuropsychologia* 47(11):2305–2313.
22. Bryant RA (2003) Early predictors of posttraumatic stress disorder. *Biol Psychiatry* 53(9):789–795.
23. Goodman M, Mitropoulou V, New AS, Sprung L, Siever LJ (2000) 436. Pathological dissociation in borderline personality disorder—the role of childhood trauma and serotonergic genes. *Biol Psychiatry* 47(8):S133–S134.
24. Varese F, Barkus E, Bentall RP (2012) Dissociation mediates the relationship between childhood trauma and hallucination-proneness. *Psychol Med* 42(5):1025–1036.
25. Lanius RA, et al. (2010) Emotion modulation in PTSD: Clinical and neurobiological evidence for a dissociative subtype. *Am J Psychiatry* 167(6):640–647.
26. Brewin CR, Gregory JD, Lipton M, Burgess N (2010) Intrusive images in psychological disorders: Characteristics, neural mechanisms, and treatment implications. *Psychol Rev* 117(1):210–232.
27. Guterstam A, Ehrsson HH (2012) Disowning one's seen real body during an out-of-body illusion. *Conscious Cogn* 21(2):1037–1042.
28. Cabeza R, St Jacques P (2007) Functional neuroimaging of autobiographical memory. *Trends Cogn Sci* 11(5):219–227.
29. Maguire EA (2001) Neuroimaging studies of autobiographical event memory. *Philos Trans R Soc Lond B Biol Sci* 356(1413):1441–1451.
30. Svoboda E, McKinnon MC, Levine B (2006) The functional neuroanatomy of autobiographical memory: A meta-analysis. *Neuropsychologia* 44(12):2189–2208.
31. Chadwick MJ, Hassabis D, Weiskopf N, Maguire EA (2010) Decoding individual episodic memory traces in the human hippocampus. *Curr Biol* 20(6):544–547.
32. Daselaar SM, et al. (2008) The spatiotemporal dynamics of autobiographical memory: Neural correlates of recall, emotional intensity, and reliving. *Cereb Cortex* 18(1):217–229.
33. Teyler TJ, Rudy JW (2007) The hippocampal indexing theory and episodic memory: Updating the index. *Hippocampus* 17(12):1158–1169.
34. Svoboda E, Levine B (2009) The effects of rehearsal on the functional neuroanatomy of episodic autobiographical and semantic remembering: A functional magnetic resonance imaging study. *J Neurosci* 29(10):3073–3082.
35. Irish M, Lawlor BA, O'Mara SM, Coen RF (2008) Assessment of behavioural markers of autonoetic consciousness during episodic autobiographical memory retrieval: A preliminary analysis. *Behav Neurol* 19(1-2):3–6.
36. Sheldon S, Levine B (2013) Same as it ever was: Vividness modulates the similarities and differences between the neural networks that support retrieving remote and recent autobiographical memories. *Neuroimage* 83:880–891.
37. Turk DJ, Heatherton TF, Macrae CN, Kelley WM, Gazzaniga MS (2003) Out of contact, out of mind: The distributed nature of the self. *Ann N Y Acad Sci* 1001:65–78.
38. Banakou D, Groten R, Slater M (2013) Illusory ownership of a virtual child body causes overestimation of object sizes and implicit attitude changes. *Proc Natl Acad Sci USA* 110(31):12846–12851.
39. Maister L, Sebanz N, Knoblich G, Tsakiris M (2013) Experiencing ownership over a dark-skinned body reduces implicit racial bias. *Cognition* 128(2):170–178.
40. Petkova VI, Ehrsson HH (2008) If I were you: Perceptual illusion of body swapping. *PLoS One* 3(12):e3832.
41. Burgess N (2006) Spatial memory: How egocentric and allocentric combine. *Trends Cogn Sci* 10(12):551–557.
42. Vogeley K, Fink GR (2003) Neural correlates of the first-person-perspective. *Trends Cogn Sci* 7(1):38–42.
43. Vogeley K, et al. (2004) Neural correlates of first-person perspective as one constituent of human self-consciousness. *J Cogn Neurosci* 16(5):817–827.
44. Ehrsson HH, Spence C, Passingham RE (2004) That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science* 305(5685):875–877.
45. Graziano MS, Cooke DF, Taylor CS (2000) Coding the location of the arm by sight. *Science* 290(5497):1782–1786.
46. Frith CD, Frith U (2012) Mechanisms of social cognition. *Annu Rev Psychol* 63:287–313.
47. Rizzolatti G, Sinigaglia C (2010) The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nat Rev Neurosci* 11(4):264–274.
48. Tulving E, Markowitsch HJ, Craik FE, Habib R, Houle S (1996) Novelty and familiarity activations in PET studies of memory encoding and retrieval. *Cereb Cortex* 6(1):71–79.
49. Tulving E, Thomson DM (1973) Encoding specificity and retrieval processes in episodic memory. *Psychol Rev* 80(5):352–373.
50. Craik FIM, Lockhart RS (1972) Levels of processing: A framework for memory research. *J Verbal Learn Verbal Behav* 11(6):671–684.
51. Godden DR, Baddeley AD (1975) Context-dependent memory in two natural environments: On land and underwater. *Br J Psychol* 66(3):325–331.
52. Dolcos F, LaBar KS, Cabeza R (2005) Remembering one year later: Role of the amygdala and the medial temporal lobe memory system in retrieving emotional memories. *Proc Natl Acad Sci USA* 102(7):2626–2631.
53. Riefer DM, Rouder JN (1992) A multinomial modeling analysis of the mnemonic benefits of bizarre imagery. *Mem Cognit* 20(6):601–611.
54. Punamäki R-L, Komproe IH, Qouta S, Elmasri M, de Jong JT (2005) The role of peritraumatic dissociation and gender in the association between trauma and mental health in a Palestinian community sample. *Am J Psychiatry* 162(3):545–551.
55. Noulhiane M, et al. (2007) Autobiographical memory after temporal lobe resection: Neuropsychological and MRI volumetric findings. *Brain* 130(Pt 12):3184–3199.