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Understanding episodic memory dynamics: Retrieval and updating mechanisms revealed by fMRI and tDCS

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ABSTRACT

This study investigates brain mechanisms in memory preservation and alteration using a three-phase design: memory encoding (Day 1), interference under fMRI (Day 2), and testing (Day 3). Thirty-one participants completed the core experiment, supplemented by a tDCS study ($n = 118$) targeting the visual cortex. Original memories were more susceptible to incorrect updating during old-background/new-object interference compared to relearning and no-retrieval conditions. Interference trials elicited heightened activation in the Inferior Parietal Lobe (IPL), Dorsolateral Prefrontal Cortex (DLPFC), and Dorsal Anterior Cingulate Gyrus (dACC) versus no-retrieval controls, and increased frontoparietal and Occipital Fusiform Gyrus (OFG) activation versus relearning. Analyzing interference trials by Day 3 outcomes revealed preserved memories correlated with stronger cingulo-opercular and frontoparietal activation (indicating effective conflict resolution), whereas updated memories showed elevated OFG activity (suggesting new sensory integration). Crucially, IPL/DLPFC activation during interference positively correlated with original memory accuracy, while OFG activation showed negative correlation. tDCS stimulation of the occipital cortex during memory reactivation significantly enhanced memory updating, confirming visual cortex involvement in contextual distortion. Findings demonstrate distinct neural profiles underlie memory outcomes: preserved memories require efficient conflict processing networks, while perceptual interference during reactivation promotes updates through sensory integration systems. This supports targeted neuromodulation approaches for memory modification, highlighting intervention potential through visual cortex engagement during critical memory phases.

1. Introduction

Memory is not a static construct, long-term memory is subject to change, with reactivation being a prerequisite for memory transformation (Misanin et al., 1968; Nader and Einarsson, 2010; Nader et al., 2000; Sara, 2000). A substantial body of evidence supports the idea of retrieval-induced memory updating as a general phenomenon, applicable to diverse memory systems, including conditioning, procedural and declarative memory (for a comprehensive review, see Lee et al., 2017). This phenomenon suggests an adaptive role in integrating recent information into the original memory trace, thereby enhancing memory's relevance (Lee, 2009). However, the occurrence and outcomes of memory updating heavily rely on the manner of reactivation, such as whether it is implicit or explicit, and whether it involves complete memory expression (Scully et al., 2017), as well as the subsequent processing of the original traces in conjunction with newly available information, such as the magnitude and valence of prediction error (Exton-McGuinness et al., 2015; Sinclair and Barense, 2019). To facilitate clinical practice in memory targeted intervention, for instance, alleviating overly intense negative memories in patients with emotional disorders, it is crucial to elucidate how the post-retrieval processing leads to specific transformations and alterations in memory (Dunbar and Taylor, 2017; Silva and Soares, 2018).

When a memory is reactivated and subsequently interfered with, it can lead to updates that involve complex cognitive processes and interactions across multiple brain regions. Memory retrieval often

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involves conscious recall and reconstruction, engaging areas such as the Inferior Parietal Lobe (IPL) (Spaniol et al., 2009; Vilberg and Rugg, 2008; Wagner et al., 2005) and extensive activation of the task demanding prefrontal cortex (Hasegawa, 2000; Hasegawa et al., 1999; Tomita et al., 1999). Furthermore, during interfering, there's a notable conflict between the original and new information, which requires resolution through either suppression or integration of memories. This process likely involves key contributions from the medial frontal lobe and cingulate cortex (Botvinick et al., 2004; van Veen et al., 2001; Weissman et al., 2003). Notably, the quality of memory reactivation can enhance or distort subsequent memories. For instance, higher activity in the posterior cingulate and rostral medial prefrontal cortex correlates with more accurate memories, while increased activation in the ventromedial prefrontal cortex and right hippocampus is linked to false memories (St Jacques et al., 2013). Interestingly, the natural modification and updating of memories often occur without the need for monitoring processes or excessive elaboration by the prefrontal cortex (Clewett et al., 2019; Zhu et al., 2019). Besides local brain region interactions, updated memories tend to form more efficient neural networks compared to unprocessed ones, suggesting a systematic reorganization of the underlying neural structures following retrieval (Bavassi et al., 2019).

However, an often neglected aspect in the study of memory updating is the importance of primary visual processing. In traditional encoding-retrieval paradigms, emerging evidence underscores the critical role that the visual cortex plays in distinguishing between true and false memories. Early sensory regions, including the visual cortex, exhibit greater activation for accurate memories compared to false ones (Dennis et al., 2015). During the encoding phase, detailed visual representations significantly contribute to the formation of precise memory traces (Brady et al., 2011; Hollingworth and Hollingworth, 2004; Naspi et al., 2021). Transcranial magnetic stimulation (TMS) of the primary visual cortex (V1) has been shown to notably reduce confidently recalled false memories related to spatial locations (Karanian and Slotnick, 2018). These findings suggest that fine-grained visual processing during encoding enhances memory accuracy, highlighting the significance of the visual cortex in the refinement of memory formation.

Within memory updating protocols employing episodic interference to disrupt consolidated engrams, activation of the visual cortex throughout the disruption interval reveals that visual information processing enables the assimilation of incoming perceptual data with entrenched mnemonic frameworks. This cognitive mechanism fundamentally differs from primary encoding processes, characterized by its neural reorganization and functional modification of stored memory representations. It can be hypothesized that visual-analytic operations occurring during memory destabilization and subsequent interference windows may constitute a neurocognitive prerequisite for schema reconfiguration processes. Supporting this hypothesis, our previous EEG studies have underscored the critical role of visual processing in memory updating. Our findings suggest that altering original memories involves an enhanced late posterior negativity (LPN) response (Pan et al., 2021). The LPN, typically observed in the posterior parietal and occipital lobes (Johansson and Mecklinger, 2003), is linked to episodic reconstruction processes where old and new information interact (Mecklinger et al., 2016; Sommer et al., 2018). This highlights a potential connection between post-retrieval updating and intensified visual scene processing.

Interestingly, the interference guiding memory updates evokes only limited conflict, as indexed by the frontal N400 component, suggesting an implicit mechanism at work (Pan et al., 2021). Additional evidence indicates that distinguishing sensory features between real and modified recognition may not be consciously accessible, implying that memory regeneration operates through a bottom-up processing mechanism (Slotnick and Schacter, 2004, 2006). Within the framework of neurocomputation and deep learning, using representational similarity analysis to decode and reconstruct memory images based on visual cortex information has emerged as a pivotal approach (Cichy et al., 2014; Cowen et al., 2014). Thus, during memory updating, the involvement of the visual cortex during the interference phase does not necessarily entail suppression efforts or fine-grained discrimination. Instead, it might reflect a more implicit and less effortful process, working in opposition to explicit control mechanisms.

From a clinical intervention perspective, visual interference also has now evolved into a distinctive approach for disrupting traumatic memories. It's worth noting that traumatic memories often possess strong visual components, and the vividness of such memories is closely tied to the intensity of induced emotions (Blix et al., 2020). This underscores the importance of considering the involvement of the visual processing cortex when targeting memory for intervention. For instance, therapeutic practices for post-traumatic stress disorder (PTSD) like Eye Movement Desensitization and Reprocessing (EMDR) require clients to recall traumatic memories and guide eye movements to alleviate emotional symptoms, aligning with the reconsolidation concept and involving visual processing (Coubard, 2016; Novo Navarro et al., 2018). Additionally, early evidence suggests that activities such as playing Tetris after recalling traumatic memories can reduce traumatic intrusions (James et al., 2015). One potential explanation offered by the authors is that the Tetris game can encroach on cognitive resources after memory recall, disrupting natural reconsolidation processes and thereby damaging the original memory. However, one study using the same high-load working memory game failed to reproduce the results (Chalkia et al., 2019). This failure may be due to the fact that the destruction of the original trace by the Tetris game following trauma evocation does not rely exclusively on its cognitive resource appropriation, but rather on the perceptual confusion of distinct episodic segments. Despite the high cognitive load of the working memory task, the lack of Tetris-like visual richness multiplicity thus discounts the effect of disruptive memory. In recent years, trauma intervention programs based on mental visual rescripting after memory recall, such as imagery-competing intervention, have also begun to show their potential in the real world (Ahmed Pihlgren et al., 2024; Iyadurai et al., 2023; Kehyayan et al., 2024; Patel et al., 2024).

In light of this evidence, we propose that the visual association area supports memory distortion by integrating old and new perceptual details during reconsolidation, as evidenced by its task-dependent activation and correlation with recall accuracy. While the prefrontal cortex and cingulate gyrus are important for conflict monitoring and explicit memory retrieval, they primarily ensure memory accuracy and integrity. In contrast, errors or changes in memory content appear more related to the visual cortex and occur through an implicit process. Based on this hypothesis, our study aims to establish predictive relationships between activity in specific brain regions and behavioral performance using functional magnetic resonance imaging (fMRI). Subsequently, we will employ neuromodulation techniques, specifically high-precision transcranial direct current stimulation (tDCS), to experimentally verify the causal roles of brain regions in memory updating. Given that sensory processing typically initiates information flow, and considering the effectiveness of visual interference interventions in clinical settings, we anticipate that continuous excitatory stimulation of the visual cortex during the post-retrieval intervention phase will significantly enhance the extent of memory modifications.

2. Study 1: the fMRI study

2.1. Methods

2.1.1. Participants

Participants voluntarily enrolled through the online experimental recruitment platform. Individuals with severe brain injury, including a history of epilepsy, brain surgery, or recent concussions, and those with confirmed mental illnesses such as schizophrenia, bipolar disorder, major depression, and anxiety disorder, were excluded. Additionally, they had to meet the safety screening criteria for MRI scans of the brain, have no metal implants, and be free from claustrophobia. In total, thirty-one healthy college or graduate students were recruited from Beijing, China (Age: 22.67 ± 4.26; Years of education: 16.93 ± 1.50; Gender ratio for male: 41.2 %). All participants signed informed consent before the experiment and received compensation. This study was approved by the Ethics Committee of the Institute of Psychology, Chinese Academy of Sciences (IPCAS-2020,004) and was conducted according to the approved guidelines.

2.1.2. *Episodic memory material*

The memory material for this study consists of three parts, learning material, interference material, and control material. Learning materials consisted of 80 monochrome combination scenarios. Each scene comprised two independent components: **background (BG)** and **core object (CO)**. The BG provided the context of the event and had no specific emotional valence (e.g., a box of a particular shape), while the CO illustrated the key content of the event and had a negative valence (e.g., a swarm of spiders). These two parts (BG+CO) constituted a scene with a specific meaning designed to create unpleasant emotional memories in participants. All scenarios were selected from a pool of candidate scenarios (120 scenarios), pre-rated by 50 college students (21 of them female, age 22.10 ± 4.90). The rating criteria included: a) discrimination ("How well can you recognize or identify the scene"), b) familiarity ("How familiar does the scene feel"), c) valence ("How pleasant it is for you to view the scene"), and d) correlation between BG and CO ("To what extent can backgrounds and objects be linked in your mind"). All these criteria were rated on a 7-point scale. For the formal study materials, scenarios with more than 6 points of familiarity and less than 2 points of discrimination were excluded. Additionally, the average valence score for each picture was between 1 and 3 (1 being very unpleasant, 7 being very pleasant). The mean valence score of the selected 80 scenes was 2.02, and the correlation of BG-CO remained at a moderate level (4.31 ± 0.89) for these materials. Additionally, 10 neutral scenes with a mean valence of 4.23 were served as fillers and practice materials.

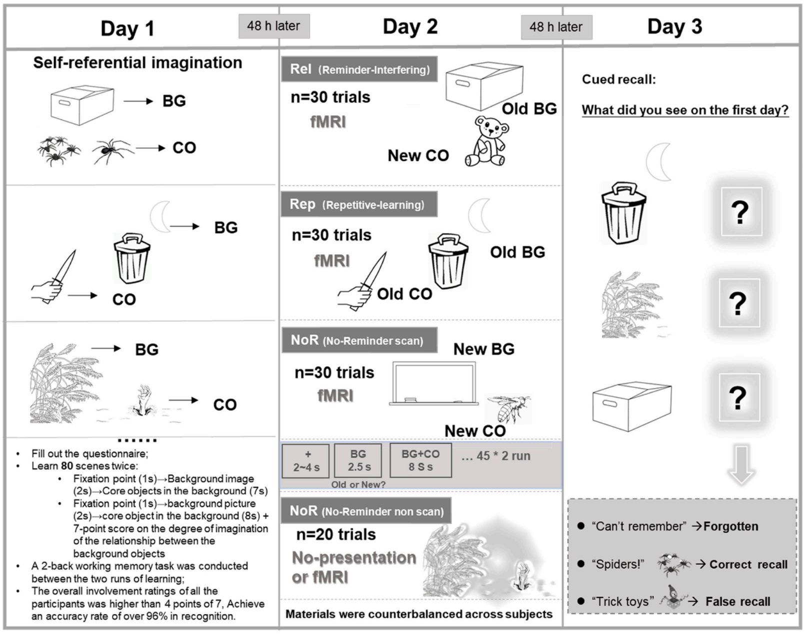
Interference materials consisted of 60 scenes with the same BG as the learning material (e.g., a specific-shaped box). However, the BG was matched with a *novel* CO with a non-negative valence (e.g., a teddy bear). In this way, 60 old BGs and 60 new COs constituted 60 independent scenes with non-negative valence. These new scenarios were evaluated by another 50 college students (20 female, age 21.10 ± 7.20 years) using a 7-point scoring system based on discrimination, familiarity, valence, and BG-CO correlation. The average valence score of each scenario ranged from 3 to 6, with a mean score of 4.24. The BG-CO correlation of these materials remained moderate (5.41 ± 0.34). None of the scenes scored less than 2 points for recognition or more than 6 points for familiarity. All these 60 scenes were divided into AB sets (30 per set), and participants were randomly assigned to one of the sets on Day 2.

The control materials consisted of 30 separate scenes, each composed of a new BG (e.g., a shopping cart) and a new CO (e.g., a thermos cup). Among them, 15 scenarios were neutral with an average valence between 3–6 and a mean of 4.89, and 15 scenarios were negative with an average valence between 1–3 points and a mean of 2.03. The correlation of BG-CO remained at a medium level (5.07 ± 0.40).

2.1.3. *Experimental procedures*

The experiment adopted a within-subject design, and the whole experiment consisted of three experiment days (Day 1: episodic learning, Day 2 (fMRI): reminder interference learning & no reminder new learning & completely repetitive learning, Day 3: testing), with an interval of about 48 h for each experimental day. The relevant experimental procedures are shown in Fig. 1.

2.1.3.1. Day 1: questionnaire and self-referential episodic learning. First, participants completed demographic information and the written informed consent. Then, all participants viewed 80 monochromatic negative scenes, consisting of neutral BG and negative CO. Participants were asked to view these scenarios in a self-referential way, imagining themselves interacting with the CO in the BG. The specific instruction is “Your task is to envision yourself in this setting, engaging with the key object as authentically as possible, either by observing or actively participating in the events”. The learning had two rounds. The sequence for the first round of viewing was as follows: first, a fixed point was shown for 1–3 s, then the BG was shown for 2 s, followed by the BG-CO combination shown for 8 s. These scenarios were presented in a random order and divided into three blocks. Participants took a rest for about 3 min between learning blocks. After the first round of learning, participants performed a 2-back digital working memory task (5 min) and rest for about 5 min to reduce inattention associated with the same type of learning task. Then the second round of learning/viewing started. In this



- Fill out the questionnaire;
- Learn **80** scenes twice:
    - Fixation point (1s)→Background image (2s)→Core objects in the background (7s)
    - Fixation point (1s)→background picture (2s)→core object in the background (8s) + 7-point score on the degree of imagination of the relationship between the background objects
- A 2-back working memory task was conducted between the two runs of learning;
- The overall involvement ratings of all the participants was higher than 4 points of 7, Achieve an accuracy rate of over 96% in recognition.

Fig. 1. Diagram of the experimental process of the fMRI study.

round, the order of viewing was as follows: First, the fixed point was presented for 1–3 s (random), then BG was presented for 2 s, BG-CO was presented for 8 s, and a scoring bar was also presented below the BG-CO combination picture. Participants were required to score the degree of imagination involvement in the scene learning on a 7-point scale. After two rounds of learning, participants' general imagination learning involvement was scored, and the overall imagination of all the participants was higher than 4 points (5.67 ± 0.79). The participants then were required to perform a rapid recognition test to determine whether they had seen the pictures with 20 new images inserted. The accuracy rate of all subjects was over 96 %, indicating the learning on the first day was generally successful.

2.1.3.2. Day 2: condition differentiation and MRI scanning. Forty-eight hours (45–51 h) after Day 1 learning, participants went to the MRI Center for the scanning experiment. Participants were informed of the sequence and process of scanning before the formal start of the scanning experiment, and the instructions for the main task were made clear to the participants outside the magnet. The participants were told that the main task of the experiment was still to be self-referential scene imagination, as did on the first day of study. During the scanning, the time flow of each learning was as follows: fixation point for 2–4 s, BG for 2.5 s, BG-CO combination for 8 s. A total of 90 scenarios were divided into two learning runs with random sequence. To enhance participants' alertness and stimulate the retrieval of imagery, we instructed them to quickly determine whether they had previously encountered the background images that appeared ('1′ for seen before, '2′ for not seen before). While the interfering procedure on the second day was still centered around "learning", our specific instructions were to "swiftly judge within 2.5 s if the background image had been seen before. However, the core focus of the experiment remained on self-referential learning". Participants were encouraged to associate the background context with the key objects, imagining real interactions with these items within the scene. Here, the accuracy of judgments about the background information served as a control for maintaining attentiveness. Participants with an accuracy rate below 50 % were excluded from the study under the assumption that they might not have engaged sufficiently in the thought processes required for retrieval. Importantly, these scenarios consisted of four conditions according to the different combination patterns of BG-CO scenarios compared with those learned on the first day:

1) **ReI condition**, Reminder-Interfering (ReI) condition, containing a total of 30 trials. These scenes had the same BG as the first day of learning to reactivate the original memory, but the BG was matched with a new CO to form the interference learning scene.
2) **Rep control condition,** Repetitive-learning (Rep) condition, containing a total of 30 trials. These scenarios had the same BG-CO combination as day one, and the subjects had to relearn the scenarios in a self-referential way. This set of scenarios served as a control condition for complete reactivation and reencoding of the initial memory in the absence of new updated information. Note here that 60 scenarios from Day 1 were divided into two sets to be assigned as either the ReI condition or the Rep condition on the second day. The subjects were presented one version at random.
3) **NoR control condition (scan),** No-Reminder (NoR) condition for fMRI scaning control, containing a total of 30 trials. These scenarios had totally different BG and CO from the first day of learning and served as the no-reminder control condition for new learning in MRI scanner.
4) **NoR control condition (non-scan),** No-Reminder (NoR) condition for behavior control, the current manipulation also implied another condition, namely, the remaining 20 scenes not selected as ReI or Rep on the first day of learning, were used as the no-reminder control (NoR) condition, where memory reactivation was not carried out on Day 2 scanning, leading to general memory fading.

2.1.3.3. Day 3: memory test. About 48 h later (45 to 51 h), all participants took an online memory test of their first day learning. Participants were asked to report the CO on the first day matching BG (a total of 80 image stimuli). Note that the newly learned BG on the second day will not be presented in the test. Participants could type the answers (the name of CO) under the corresponding BG pictures without a time limit, and they were particularly reminded to report the objects on day 1 and encouraged to give a specific answer, even if they weren't confident about the answer. For the collected recall test data, all responses were classified into three categories: (1) **Correct recall**: the key information of the CO matched by the Day 1 BG was correctly recalled (e.g., report a spider or a group of spiders under the corresponding BG); (2) **False recall**: the CO in this background is falsely recalled (e.g., report a tricky toy under the corresponding BG; if the toy bear was reported, that is, the complete memory invasion, is also counted as false alarm) . Although this consolidation blurs the precision of understanding different forms of error memories to some extent, in our data, instances of memory intrusions were actually quite rare, with no more than two intruded items per participant. Because participants were explicitly asked to recall scenes from the first day, they might recall features that are characteristic of intruded items but do not fully align with the core of what was newly learned on the second day, thus being categorized as false memories. In fact, if participants clearly knew it was the second day's memory but had little recollection of which day it was, they would report forgetting. As will be stated below. (3) **Forgotten**: claims to completely forget the object of the first day (participants are likely to claim to have forgotten the objects on the first day, but report what they saw on the second day, which is recorded as forgetting). The correct recall (code as 1), false reall (code as 2), and forgetting (code as 0) of the report text are independently classified by two research assistant, and the consistency is checked by Cramer's V as 0.99, $p < 0.001$. If there is any inconsistency, the final conclusion will be determined through comprehensive negotiation.

2.1.4. Magnetic resonance scanning and pre-processing

The whole brain imaging data were collected using a GE 3.0 T magnetic resonance scanner (GE Discovery MR750) in the Brain Imaging Center, Institute of Psychology, Chinese Academy of Sciences. Participants lay flat in the scanning room, with rubber earplugs to reduce noise and foam pads attached to their heads to reduce head movement. All participants completed the 8-minute resting-state fMRI scan first. During the resting scanning process, subjects were required to look at the fixation point in the center of the screen and keep relaxed to adapt to the environment inside the magnet (The resting-state scan was required by the center's shared data project, and the relevant data were not analyzed or used in this study). Then, there was task-mode fMRI scanning, during which the participants completed the (reminder interference) learning. This was followed by the first round of the main task (task-mode fMRI scanning), which lasted about 10.05 min, with 319 images obtained each time. Then the T1 structural image was scanned for about 5 min, followed by the second round of the main task for about 10.05 min. The final T2 image was scanned for about 5 min. The scanning time was approximately 40 min. Echo-planar imaging (EPI) sequence was used for the functional images of the resting state and task scanning, with the following scanning parameters: repetition time (TR) = 2000 ms, echo time (TE) = 30 ms, flip angle (FA) = 90°, slice thickness = 3.5 mm, number of slices = 37, FOV = 22.4 cm, voxel size = $3.44 \times 3.44 \times 4\ \text{mm}^3$, and acquisition matrix = 64 × 64. A sagittal 3D T1 Fast SPGR sequence was used for structural images, with scanning parameters: inversion time (TI) = 450 ms, echo time (TE) = Min Full ~3.2 ms, flip angle (FA) = 12°, FOV = 25.6 cm, slice thickness = 1 mm, voxel size = $1 \times 1 \times 1\ \text{mm}^3$, and acquisition matrix = 256 × 256.

SPM12 (http://www.fil.ion.ucl.ac.uk/spm/), Xjview (http://www.alivelearn.net/xjview), DPABI V3.1 (http://rfmri.org/dpabi) and BrainNet Viewer (Xia et al., 2013) under MATLAB 2016a (https://www.mathworks.com) were used to perform data pre-processing, statistical analysis, and visual presentation of fMRI data. The first 10 s of each scanning run were removed in data processing to reduce the initial scan interference. Data pre-processing included the following steps: (1) Slice Timing Correction; (2) Realign, during which every frame image in each run was aligned with the first frame image according to a certain algorithm. Participants with translational rotation greater than 3 mm or/and more than 3° in roll rotations were plan to be removed. Under this criterion, however, no participants in the current dataset were excluded; (3) Coregister, registering the average functional image of each subject with its own T1 structural image; (4) Normalize space. The functional image and the structural image were registered to the MNI standard space, and the functional image data were resampled to $3 \times 3 \times 3$ mm^3. Gaussian smooth (using an 8 mm Full Width at Half Maximum, i.e., FWHM Gaussian kernel) was applied to the data.

2.1.5. Statistical analysis

For behavioral data, repeated measurement ANOVA was used to compare the learning involvement on the first day and memory performance on the testing day according to different manipulations on the second day (ReI, Rep, NoR). The memory performance classification consistency (correct recall, false recall, and forgetting) for all answers were evaluated by two raters. The two raters were highly consistent (Cramer's $V = 0.99$, $p < 0.001$), and inconsistent answers were discussed together and reconfirmed.

In the statistical analysis of fMRI data, the generalized linear model (GLM) was used for individual-level analysis. Six rows of pre-generated head motion parameters were controlled as covariables, and high-pass filtering (128 s) was used to remove low-frequency drift. Contrasts were defined to calculate the brain activation difference of all subjects under the conditions of ReI, Rep, and NoR. Pairwise comparisons of the three conditions were set (i.e., ReI – Rep, ReI – NoR).

Furthermore, the ReI trials were divided into (1) Reactivation-Distorting original memory trials (**ReI-Change-Origin**), that is, the retrieval interference manipulation on the second day resulted in false recall or forgetting of the original memory on the first day; and (2) Reactivation-maintain original memory trials (**ReI-Maintain-Origin**), that is, the retrieval manipulation on the second day did not interfere with the original memory of the individual, and the individual correctly recalled the objects corresponding to the background on the first day. A direct contrast between these two conditions was set (i.e., ReI-Change-Origin vs. ReI-Maintain-Origin). We identified significant activation clusters using a voxel-level threshold of $p < 0.001$ and applied False Discovery Rate (FDR) correction at the cluster level (< 0.05), requiring clusters to contain more than at leat 20 voxels (the FDR-C values under different contrasts would be specified in the results section).

Additionally, neural-behavior regression analysis was performed. The brain regions with significant contrast differences on the manipulation day (Day 2) from contrast above were defined as regions of interest (ROIs). The contrast value of these ROIs was extracted to predict the individual's recall performance on the testing day. This regression analysis aimed to investigate whether the activation level of specific brain regions in the reconsolidation (reminder-interference) stage can modulate the retention/updating of the original memory.

3. Results

3.1. Effect of reminder-induced interference on memory

Interfering learning after a reminder induces significant memory distortion. A significant main effect for the correct recall rate on the testing day was observed, $F_{(2,60)} = 39.89$, $p < 0.001$, $\eta_p^2 = 0.57$. Post-hoc pairwise comparisons between conditions revealed the reminder-interfering (ReI) condition exhibited significantly lower correct recollection than the repetitive-learning (Rep) condition ($p < 0.001$) and the no-reminder behavior control (NoR) condition ($p = 0.029$). Consistently, false recall under the three conditions differed significantly, $F_{(2,30)} = 35.13$, $p < 0.001$, $\eta_p^2 = 0.54$, with the false recall rate in the ReI condition significantly higher than that in the Rep ($p < 0.001$) and NoR control ($p < 0.001$) conditions. The forgetting rate also differed significantly, $F_{(2,60)} = 36.37$, $p < 0.001$, $\eta_p^2 = 0.55$.

Post-hoc comparisons revealed the NoR control condition exhibited the highest forgetting rate, followed by the ReI condition ($p < 0.001$), while the Rep condition showed the lowest forgetting rate ($p < 0.001$). Given no significant difference in recognition accuracy and self-rated learning on Day 1 (ReI, Rep, NoR), reminder-interfering learning (ReI) on Day 2 appears to be the main factor causing their memory performance decline for Day 3's testing. See Fig. 2a for a visual representation of memory performance across conditions.

3.2. Neural correlates of reminder interference processing

Here, we compare the ReI condition with two different control conditions: the NoR (i.e., condition without reminder, completely new learning), and Rep (i.e., repeated learning). Comparing with the NoR control the ReI condition revealed significantly greater activation in the bilateral dorsolateral prefrontal cortex (DLPFC, L: $x = -39$, $y = 18$, $z = 36$; R: $x = 45$, $y = 24$, $z = 24$), medial prefrontal cortex, especially the dorsal anterior cingulate gyrus (dACC, $x = -3$, $y = 30$, $z = 39$), bilateral inferior parietal lobes, including the angular and supramarginal gyri (IPL, L: $x = -36$, $y = -57$, $z = 51$; R: $x = 33$, $y = -51$, $z = 36$), and left middle temporal gyrus (MTG, $x = -60$, $y = -30$, $z = -15$); Compared to the Rep, the ReI condition activated more areas in the left middle/inferior frontal gyrus ($x = -48$, $y = 30$, $z = 21$), superior parietal lobule (SPL, L: $x = -24$, $y = -57$, $z = 30$; R: $x = 27$, $y = -66$, $z = 39$), and more occipitotemporal cortex, including the left inferior temporal gyrus (ITG, $x = -48$, $y = 60$, $z = -15$) and occipital fusiform gyrus (OFG, L: $x = -27$, $y = -84$, $z = 12$; R: $x = 33$, $y = -39$, $z = -24$). See Table 1 and Fig. 3a for relevant results.

Furthermore, dividing the ReI condition into two sub-conditions based on final memory performance revealed that ReI-Maintain-Origin activated the precuneus /posterior cingulate ($x = -6$, $y = -51$, $z = 18$), MTG ($x = 45$, $y = -18$, $z = 15$), ACC ($x = -12$, $y = 45$, $z = 18$), and supramarginal gyrus ($x = -45$, $y = -51$, $z = 27$). In contrast, ReI-Change-Origin activated the wide inferior occipital gyrus (IOG) and OFG (L: $x = -39$, $y = -84$, $z = -9$; R: $x = 30$, $y = -78$, $z = -15$) as well as the Orbital gyrus ($x = -21$, $y = -30$, $z = -6$). See Table 1 and Fig. 3b for relevant results.

3.3. Predictive factors of memory performance

We defined brain areas with significant activation of ReI > NoR and ReI > ReP as regions of interest (ROIs) and extracted contrast values to conduct regression analysis to predict memory recall performance on the testing day. In the ReI > NoR contrast, activation of the bilateral IPL (including the angular gyrus and marginal supramarginal gyrus) during the interference learning phase positively predicted the accuracy of an individual's memory performance on the testing day (left: $\beta = 0.62$, $p < 0.001$; right: $\beta = 0.44$, $p = 0.013$). Activation of the left DLPFC also significantly predicted the correct recall rate of the original memory ($\beta = 0.38$, $p = 0.034$). More activation of the IPL and DLPFC during the interference learning phase corresponded to better recollection of the original memory, reflecting resistent to memory distortion following the reminder. In contrast, activation of the dACC negatively predicted false memory ($\beta = -0.40$, $p = 0.028$). Stronger activation of the dACC was associated with lower false reporting of the original memory the next day. In the ReI > ReP contrast, stronger activation of the right OFG was associated with lower memory accuracy on the next day ($\beta = -0.34$, $p = 0.049$). For illustration, see Fig. 3c.

3.4. Results summary

These results from fMRI perspective indicate that different neural

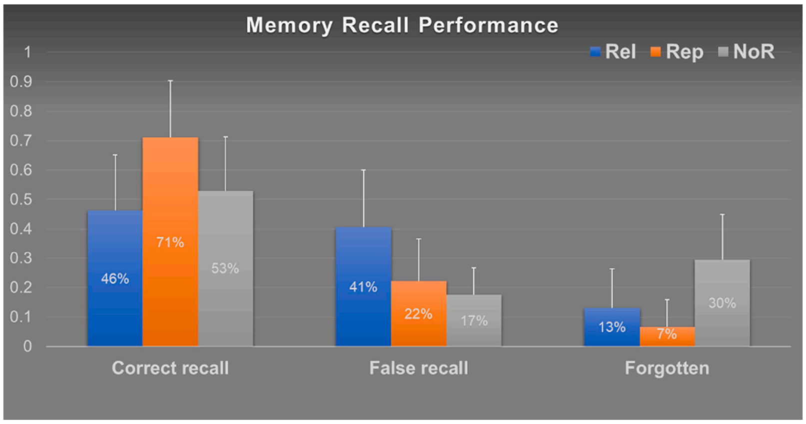


Fig. 2. Memory performance for the Day 1 across conditions / manipulations from the Day 2. Reminder-Interfering (ReI) condition: pictures that were reminded on the day2 by presenting with the same background as on the day1 while being interfered with new object matching; Repetitive-learning (Rep) condition: pictures that were completely repeated the day2; No-Reminder (NoR) condition: pictures that not showing up or being reminded the day2. The ReI condition produced the most updating errors in memory (False recall), the Rep condition had the highest recall accuracy, and the NoR condition had the highest forgetting rate. The error line is the standard error.

activity patterns following a reminder guide distinct directions of original memory change. Stronger activation of the original memory (IPL) and the activation of the conflict monitoring system (dACC), accompanied by more volitional effort encoding (DLPFC), induced retention and enhancement of the original memory. While limited conflict monitoring, and more refined visual scene encoding for new sensory input (mainly involving OFC) can induce memory errors, leading to directed updating or distortion in the original memory. The fMRI evidence indicates that the involvement of the visual cortex during the memory disruption phase is crucial for promoting memory updating. Therefore, targeting the activation of the occipital cortex during the post-retrieval interference phase may serve as a potential strategy to enhance memory updating.

4. Study 2: the tDCS study

4.1. Methods

4.1.1. Participants

Participants voluntarily enrolled through the online experimental recruitment platform. Healthy adults aged 18 to 35 years old were recruited. Exclusion criteria included: a) Concussion in the last six months; b) Chronic headache; c) Chronic insomnia; d) Severe mental illness, including diagnosed schizophrenia, major depression, obsessive-compulsive disorder, phobias, panic attacks, post-traumatic stress disorder, etc.; e) Have taken antipsychotic drugs in the past two months; f) A history of epileptic seizures within immediate family members (including parents and siblings). The enrolled subjects were interviewed by phone before the formal experiment to ensure that they did not meet any of the exclusion criteria. A medium effect size ($f = 0.35$) was assumed in the fixed four-factor design of one-way ANOVA, which required 92 subjects to achieve 80 % statistical power, meaning at least 23 subjects per group. Considering the possible data loss due to various technical reasons, it was planned to recruit 30 subjects for each group.

Participants were randomly assigned to four experimental groups: A) reminder interference + Occipital tDCS (ReI_tDCS), B) reminder interference + Occipital sham (ReI_Sham), C) non-reminder interference + Occipital tDCS (NoR_tDCS), D) non-reminder interference + Occipital sham (NoR_Sham). During the experiment, one participant from the ReI_Sham group and one from the NoR_TDCS group did not complete the memory task on the test day on time, so they could not be included in the statistical analysis. This resulted in a final number of participants as follows: ReI_tDCS $n = 30$, ReI_Sham $n = 29$, NoR_tDCS $n = 29$, NoR_Sham $n = 30$. There was no significant difference in age ($F_{(3114)} = 0.80$, $p = 0.497$), years of education ($F_{(3,97)} = 2.07$, $p = 0.108$), and gender of the four groups ($\chi^2 = 3.57$, $p = 0.191$).

4.1.2. Self-reported questionnaire

To account for the between-group design and future applications of memory regulation, we collected information on participants' emotional states and general memory status. Specifically, the subjects participated in filling out two questionnaires:

1) The Depression, Anxiety and Stress Scale (DASS-21), a simplified Chinese version (Wang et al., 2016), containing 21 items used to evaluate an individual's general mood status related to depression, anxiety, and stress.
2) The survey of autobiographical memory (SAM) by Palombo et al. (2013), in a Chinese-translated version. It includes 36 items across four dimensions of episodic memory, semantic memory, spatial navigation, and future imagination, used to assess trait mnemonics in everyday life.

4.1.3. Experimental procedures

The associated experimental flow diagram is shown in Fig. 4a.

4.1.3.1. Day 1: online supervised scenario learning tasks. The Day 1 learning procedure was the same as the fMRI task, but it did not take place in the laboratory. Instead, participants viewed and learned negative scenes in their own places. The learning materials were still BG and CO combinations, and the learning method was self-referential. To control the quality of online learning, the participants' learning performance was checked immediately, including self-learning assessment, which required them to recall the general imagination involvement during the learning (1= very hard to imagine, 7 = very easy to imagine), and self-rated memory performance after the learning (1= nothing remembered, 7 = all remembered). In addition, one specific BG scene (all subjects were the same) was selected, and participants were required to recall the corresponding objects of this specific BG immediately. This particular image is not presented again in the following experiments. Participants could proceed to the next stage of the experiment only when their recall was correct and the subjective ratings of learning were higher than 3.

4.1.3.2. Day 2: tDCS/Sham manipulation and reminder/no-reminder interference. The second experimental day was carried out in the laboratory with an interval of about 48 h (within 4 h error) from the first learning day. This day included tDCS/Sham manipulation and

Table 1
Neural Correlates of reminder interference processing.

Brain areas (voxel-level $p < 0.001$, cluster-level $q_{FDR} < 0.05$)	R/L	x	y	z	t value	Cluster size
Activated brain regions of the ReI condition to two control conditions						
ReI learning - NoR Control learning (FDRc: 36)						
Inferior Frontal Gyrus/Middle Frontal Gyrus (Dorsolateral prefrontal cortex)	L	−39	18	36	9.05	1222
Inferior Frontal Gyrus/Middle Frontal Gyrus (Dorsolateral prefrontal cortex)	R	45	24	24	7.56	417
Medial Frontal Gyrus/Limbic Lobe (Dorsal anterior cingulate cortex)	L/R	−3	30	39	8.02	534
Inferior Parietal Lobule/ Angular/Supramarginal Gyrus	L	−36	−57	51	9.05	556
Inferior Parietal Lobule/ Angular/Supramarginal Gyrus	R	33	−51	36	8.03	333
Middle Temporal Gyrus	L	−60	−30	−15	5.62	37
ReI learning - ReP Control learning (FDRc: 46)						
Middle Frontal Gyrus/Inferior Frontal Gyrus	L	−48	30	21	6.52	278
Precuneus/ Angular/Superior Parietal Lobule	L	−24	−57	30	6.46	308
Superior Parietal Lobule/ Angular/ Occipital Gyrus	R	27	−66	39	5.73	353
Fusiform Gyrus /Inferior Temporal Gyrus	L	−48	60	−15	6.37	64
Occipital Fusiform Gyrus	L	−27	−84	12	5.52	100
Fusiform Gyrus	R	33	−39	−24	5.14	46
Specific brain activation within the ReI condition to differential memory outcomes						
ReI-Maintain-Origin > ReI-Change-Origin (FDRc: 21)						
Precuneus/ Posterior cingulate cortex	L/R	6	−51	18	5.46	56
Middle Temporal Gyrus	R	45	−18	15	6.02	26
Superior Frontal Gyrus Medial Segment /Anterior Cingulate Cortex	L	−12	45	18	5.51	21
Supramarginal Gyrus/ Angular	L	−54	−51	27	4.03	25
ReI-Change-Origin > ReI-Maintain-Origin (FDRc: 29)						
Inferior Occipital Gyrus /Occipital Fusiform Gyrus	L	−39	−84	−9	6.06	248
Orbital gyrus	L	−21	30	−6	6.73	65
Occipital Fusiform Gyrus	R	30	−78	−15	4.24	29

reminder/no-reminder interference learning stages, with a between-subject (four groups) design. The environment on Day 2 was completely different from the original memory learning on the first day, excluding the implicit memory reactivation caused by the same coding scene. Thus, the reactivation of the original memory was completely dependent on the content of the learning material, specifically the consistent BG picture. Before the experiment, subjects were required to sign informed consent to inform them of the safety and possible sensations during tDCS.

The tDCS procedure as follows: The electric current stimulator was the high-definition constant current stimulator (HD-tDCS) NSS18, NeuStim, Neuracle Technology Co., Ltd., Changzhou, China. A 4 × 1 ring electrode was used, fixed in a 32-channel EEG localization cap (a positive center electrode covering the target brain region and surrounded by four negative electrodes). The central electrode (anode) was placed on Oz according to the international 10–20 EEG system, and the four cathode electrodes were about 3.5 cm in diameter from Oz, corresponding to PO3, PO4, PO9 and PO10 positions. The stimulus location was chosen taking into account the results of previous fMRI studies suggesting that disturbed memory requires occiput temporal visual processing during the retrieval interference phase. We performed a surface projection of the pattern of ReI-Change-Origin memory in Study I using Mango (https://mangoviewer.com/). In addition, SimNIBS software (Saturnino et al., 2015) was used to evaluate the cortical electric field induced by HD-tDCS based on the finite element model of the brain current with an MRI template, and it was determined that the generated current could stimulate the extensive visual cortex including the occipital fusiform gyrus, see Fig. 4b

The procedure for tDCS or sham tDCS is as follows: after the preparation, the participant was seated in front of the computer screen, and the electrode with saline was attached to the scalp, which was covered with a scalp cap. First, the electrode position was measured and marked. Then, the stimulation was started in the tDCS group, with the following parameters: current intensity of 1 mA (Oz=1 mA; PO3, PO4, PO9 and PO10 = - 0.25 mA), stimulating for 10 min continuously. In the sham group, tDCS stimulation started, but stopped automatically after 20 s, with a progressive feeling of tingling and itching, which made it hard for participants to distinguish it from real tDCS. Participants were asked to close their eyes while receiving the stimulus, after the end of stimulation, they were told to start the picture learning immediately.

The learning materials on the second day were also BG and CO combinations, and participants learned these scenes in the same self-referential way as on Day 1. Importantly, the learning content was divided into two categories: a) ReI: reminder interference learning, in which the BG was the same as the first day, but the BG was matched with a new CO to form the interference learning scene; b) NoR: non-reminder interference learning, in which a new BG was presented with a new CO to form the non-reminder interference learning scene, which combined with true and sham stimuli, four intersubject conditions were formed. The same quality control procedure as the first day was applied on Day 2, including recalling the learning scenario (a specific scene with the same BG, all subjects were the same), self-rated learning (learned in a self-referential manner), and a subjective assessment of the self-rated scene.

4.1.3.3. Day 3: memory test. The Day 3 memory test procedure was similar to the fMRI study. Participants were required to recall the objects corresponding to the background on the **first** learning day, and their answers were assessed by two raters as 1) correct recall or 2) false recall. The two raters had high consistency (Cramer's $V = 0.97$, $p < 0.001$), and inconsistent answers were discussed together and reconfirmed.

4.1.4. Statistical analysis

In the analysis of memory performance, the correct recalls and the false recall rate was selected as the main dependent variable. A 2 (Reactivation: ReI/NoR) x 2 (tDCS: tDCS/Sham) between-group ANOVA was performed. In addition, we performed Pearson correlations between memory performance and individual questionnaire scores and compared differences between manipulation groups.

5. Results

5.1. Occipital tDCS effects on memory updating

The tDCS experiment included four experimental groups: (1) reminder interference + Occipital tDCS (ReI_tDCS), (2) reminder interference + Occipital sham (ReI_Sham), (3) Non-reminder interference + Occipital tDCS (NoR_tDCS), (4) Non-reminder interference + Occipital Sham (NoR_Sham). We found a significant main effect of reactivation, with ReI conditions showing significantly lower correct recall than NoR group, $F_{(1114)} = 16.53$, $p < 0.001$, $\eta_p^2 = 0.127$ and higher false recall than NoR group, $F_{(1114)} = 16.61$, $p < 0.001$, $\eta_p^2 = 0.128$, indicating that in the intersubject design, the post-retrieval interference also leads to impairment of original memory. The main effect of tDCS was not

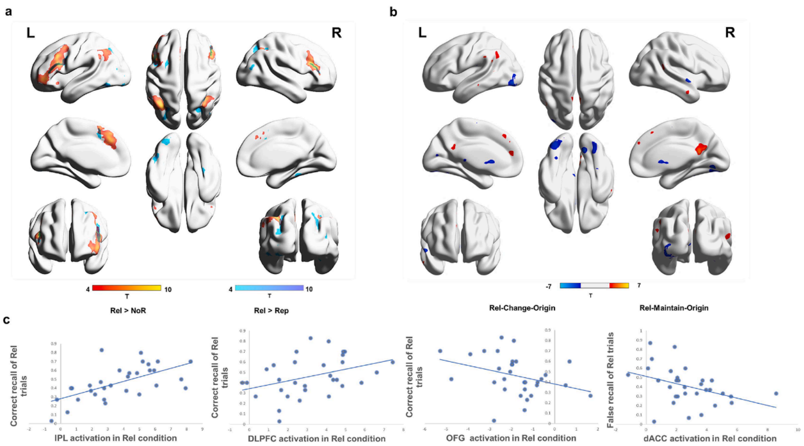


Fig. 3. Neural Correlates of reminder interference processing. a) shows the activation of the brain region in the ReI condition compared with the two control conditions, and b) shows the distinguished activation pattern of the ReI processing that was related to later maintained and later changed memory; c) shows that activation in the Inferior Parietal Lobe (IPL) and Dorsolateral Prefrontal Cortex (DLPFC) in the ReI condition positively predicted correct recall, whereas activation in the Occipital Fusiform Gyrus (OFG) negatively predicted memory performance, and activation of Dorsal Anterior Cingulate Gyrus (dACC) in ReI predict fewer false memories.

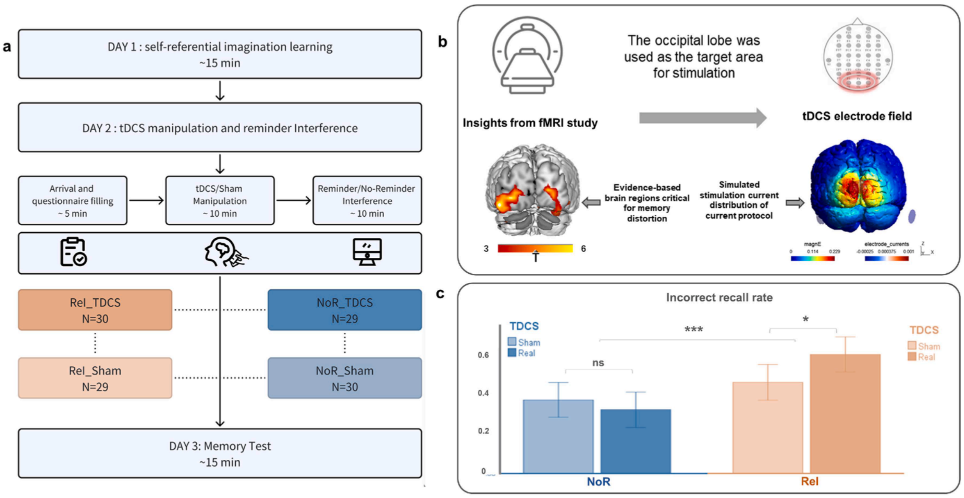


Fig. 4. Procedure and main results of the study 2 of tDCS experiment. a) The main process of the experiment; b) The key occipital regions where memory was modulated from Study 1 and the results of tDCS current simulation, in which the logic of using Study 1 to guide target selection of study 2 is presented; c) The main findings of the tDCS study, regarding the main effect of memory retrieval and the interaction with the tDCS, the occipital neuromodulation acted as a lever on memory distortion; *: $p < 0.05$; ***:$p < 0.001$; the error line is the 95 % confidence interval.

significant $F_{(1114)} = 1.01$, $p = 0.371$, indicating that tDCS in the visual cortex per se did not distort or interfere with the original memory. Importantly, we observed an interaction between tDCS and memory reactivation, $F_{(1114)} = 4.85$, $p = 0.0036$, $\eta_p^2 = 0.038$. Post-hoc tests showed that the recall accuracy of ReI_tDCS was significantly lower than that of the ReI_Sham, $t_{(57)} = 2.20$, $p = 0.032$. However, for the two non-reminder groups, whether the stimulus was real or not did not affect the final memory performance, $t_{(57)} = 0.79$, $p = 0.443$. The relevant results are presented in Fig. 4c.

5.2. Self-rating questionnaire and behavioral performance

Pearson correlation was used to find a negative association between depression level and self-reported episodic memory ability ($r = -0.226$, $p = 0.024$). While, no reliable correlation was found between self-rated memory ability and objective memory performance, either at the general level or at the group level.

5.3. Results summary

The current study indicated that post-retrieval interference steadily impaired the original memory, even in a between-group design. Furthermore, the data has proved the role of visual cortex is crucial to achieve the interference updating of reactivated memory. The interaction effect demonstratec the leverage of occipital tDCS in facilitating memory changes. For tDCS to work in the visual cortex, it depends in part on the reactivation of the original memory and the interference input. These results provide a new perspective of "bottom-up" intervention for the modification and update of memory.

6. Discussion

Understanding the neural underpinnings that orchestrate post-retrieval memory modification bears substantial clinical relevance. Our research elucidates that the vigorous engagement of fundamental memory retrieval processes, evidenced by increased activity within the IPL, in conjunction with conflict surveillance in the dACC, and deliberate memory re-encoding facilitated by the DLPFC, is conducive to memory preservation. On the contrary, feeble memory activation, diminished conflict monitoring, and intricate incorporation of novel information, particularly engaging the OFG, precipitates memory inaccuracies and diminishes original mnemonic strength. The critical function of the visual cortex in the process of memory manipulation is further substantiated via a neuromodulation investigation, wherein retrieval interference and tDCS targeting the visual cortex serve as levers to amplify memory updating. These findings corroborate the proposition that memory traces are amenable to alteration through weak initial trace activation and enhanced processing of contemporaneous information, underscoring the significance of visual engagement. This perspective paves the way for the formulation of pioneering clinical interventions, rooted in the tenets of memory reconsolidation, thus offering promising therapeutic prospects for memory-related disorders.

The data supports the idea that memory traces can be effectively modified when an initial memory is partially activated by context cues and new information is processed simultaneously. This aligns with the concept of memory reconsolidation and opens avenues for clinical interventions based on this principle (Lee et al., 2017). By focusing on declarative memory, our experimental design integrates picture-scene pairs and self-relevant processing, enhancing ecological validity and providing a flexible model for studying memory updates (Pan and Li, 2021). Neurally, our results show that attempts to retrieve memories using incomplete cues along with novel interfering inputs trigger a distinct activation pattern in the posterior parietal cortex, particularly in the IPL. This reinforces the IPL's established role in episodic memory retrieval, as seen in previous studies (Spaniol et al., 2009; Vilberg and Rugg, 2008; Wagner et al., 2005). Activations in the medial prefrontal cortex and ACC reflect neural conflict from processing familiar and novel information together, similar to findings in cognitive conflict tasks (Botvinick et al., 2004; van Veen et al., 2001; Weissman et al., 2003). Meanwhile, increased activity in the DLPFC corresponds to the demands of managing conflicting cognitive tasks, consistent with research on executive function (Botvinick et al., 2001; MacDonald et al., 2000). Correlations derived from our data further illuminate that the activation of the ACC and DLPFC correlates positively with memory accuracy, implying their direct involvement in enhancing recollection fidelity. Conversely, activation of the ACC shows an inverse association with the occurrence of false memories, suggesting that minimizing conflict monitoring and reducing high-level processing activities are imperative when the aim is to diminish the strength of the original memory trace.

During the process of memory retrieval, compared to repetitive learning, interference tends to elicit a significantly heightened level of visual reconstruction processing. This increased activity is particularly notable in brain regions such as the occipitotemporal cortex and the fusiform gyrus, as supported by a wealth of research (Spagna et al., 2021; Winlove et al., 2018). These areas are deeply involved in the detailed reprocessing of visual information that occurs when memories are retrieved under conditions of interference. Our regression analyses underscore the critical role of the occipital lobe (especially the OFG) in generating visual imagery and in the reconstructive updating of memories. The data reveal an intriguing inverse relationship between the activation levels within this region and the retention of original memories. We propose that visual activation differences across conditions reflect distinct computational demands rather than uniform perceptual processing. Specifically, enhanced OFG involvement during ReI versus passive repetition likely arises from the necessity to reconfigure existing visual representations when integrating novel information into labile memory traces—a process distinct from stabilization during mere rehearsal. In contrast, the absence of occipital activation differences between ReI and no-retrieval learning suggests comparable visual and novelty processing loads across conditions, despite divergent cognitive goals: While NoR engages the OFG for de novo encoding of novel associations unconstrained by prior memories, ReI repurposes OFG to resolve representational conflicts between reactivated and interfering traces. This functional divergence is orchestrated by interactions with higher-order networks—specifically, prefrontal and cingulate regions recruited during ReI coordinate conflict monitoring with OFG-mediated representational plasticity, enabling dynamic adaptation of memory systems to competing task demands.

The current analysis further categorized trials based on whether memories were altered. Trials with modified memories showed less activation in the precuneus and supramarginal gyrus compared to unchanged memories. These regions typically activate during detailed recall but are less important for simpler recognition tasks (Cabeza, 2008; Elman and Shimamura, 2011; Rugg and King, 2018). Increased activity in the frontoparietal areas suggests a careful processing approach that refines memory storage rather than changing the original memory trace (Simons and Spiers, 2003; Wing et al., 2020). Thus, memories that change seem to require only subtle reactivation during retrieval interference, without engaging brain areas involved in effortful recall. Even reactivating the original memory with a prediction error is key for reconsolidation (Exton-McGuinness et al., 2015), large deviations from expected outcomes can lead to the formation of new memory traces, rather than changing the original memory (Hupbach et al., 2007). Prior research across comparable paradigms (Pan et al., 2021) and diverse memory modalities (Li et al., 2017) underscores the importance of incomplete memory reactivation for promoting memory malleability. This concept is further elaborated upon in theoretical reviews (Sinclair and Barense, 2019).

Furthermore, our data illuminates that trials which underwent subsequent memory updating demonstrated augmented activation in brain regions profoundly associated with the processing of visual perceptual features, again the inferior occipital gyrus and the occipital fusiform gyrus. These areas are pivotal in higher-level visual processing, notably in object recognition, harboring zones sensitive to intricate visual stimuli encompassing faces, places, and objects. They are deeply involved in the processing of elaborate visual scenes and objects (Grill-Spector and Weiner, 2014; Kanwisher and Yovel, 2006). Such findings suggestively articulate that for memory updating to ensue, the learning and processing of visual attributes of novel scenes during the retrieval interference phase is indispensable. This learning is not merely a case of de novo acquisition but rather an integrative process that amalgamates both novel and existing scene information. Given that the implicated brain regions are linked with higher-order visual processing rather than the most rudimentary visual cortex (Malach et al., 1995; Schultz, 2005), this further underscores the sophisticated nature of the visual integration required for memory update.

It is worth noting that insufficient processing in the visual cortex has traditionally been linked to the formation of false memories, where familiar images lack the detailed richness of genuine visual experiences (Naspi et al., 2021). However, within memory updating paradigms, the role of the visual cortex gains a new significance. Post-retrieval processing of visual information becomes a critical mechanism for revising and transforming existing memories. This insight reveals that the visual cortex, rather than merely contributing to memory inaccuracies, actively participates in refining and adapting stored memories, highlighting its potential in the dynamic process of memory updating.

The visual cortex's ability to modify or overwrite established memories resonates with the principles of memory reconsolidation, a process during which recalled memories transiently become unstable and susceptible to change. Specifically, in our tDCS experiment, it has been shown that without initial memory retrieval interference, stimulating the visual cortex alone does not induce modifications to the original memory. This highlights the necessity for a memory recall procedure to initiate changes, emphasizing the vital role of integrating visual processing of both old and new information for effective memory updating. These findings echo those of previous studies, illustrating how instances of later memory alteration correlate with intensified activity in the visual cortex. This heightened activation aligns with observations of an amplified neuroelectric response, known as the late posterior negativity, in posterior brain areas, especially at the occipital electrodes, reflecting the brain's engagement in memory modification processes (Pan et al., 2021).

The integration of memory retrieval with visual tDCS findings not only demonstrates the potential role of visual processing in memory updating but also opens up new possibilities for personalized therapeutic interventions. By shifting focus from the traditionally emphasized prefrontal cortex and top-down regulatory mechanisms, which have been central in conventional neuromodulation research (Javadi and Cheng, 2013; Javadi and Walsh, 2012), our investigation highlights the potential of the occipital cortex in memory modulation. This innovative "bottom-up" strategy, reminiscent of techniques used in EMDR and imagery-competing interventions, introduces novel pathways for managing negative memories through visually mediated approaches. One might expect that, in comparison to boosting prefrontal and inhibitory control capabilities, this approach of modifying memories via visual interference during the retrieval-interference phase could proceed more implicitly and with reduced emotional discomfort.

Expanding on this perspective, the potential for cross-modal interventions becomes evident, particularly the transition from language-based therapies (such as talk therapy) to non-verbal psychological treatments. For instance, exposure therapy and virtual reality therapy leverage visual stimuli to remodel fear-related memories. These methods capitalize on the plasticity of visual memory traces, aiming to replace traumatic or maladaptive recollections with less distressing alternatives (Carl et al., 2019). The versatility of the visual cortex in updating memories suggests promising applications in clinical settings, like PTSD, where visual memories play a significant role. Visual tDCS combined with memory retrieval tasks might offer a non-invasive way to weaken the intensity of traumatic memories, thereby reducing their emotional impact. Additionally, these strategies could be adapted to help individuals suffering from anxiety, depression, or other mood disorders accompanied by enhanced pathological memories. It should be emphasized that, based on our results within the reconsolidation framework, the visual modification strategy appears to be contingent upon the proper reactivation of the original memory. Additionally, it requires the establishment of an alternative yet stable environment that diverges from the initial traumatic setting while offering enough stability and safety. Only under these conditions can the memory be effectively rewritten. This approach underscores a key aspect that most trauma interventions must address.

It is important to acknowledge several limitations of our study, which focused exclusively on visually encoded episodic memories. The use of image pairs as memory materials means that properties such as discriminability and the association between backgrounds and objects can influence recall performance. While we attempted to standardize these materials through a screening process based on ratings, the inherent attributes and associations within the images could only be partially controlled. This approach limits our ability to balance these factors at the individual participant level. Moreover, the use of black-and-white images restricts the direct applicability of our findings to authentic traumatic memories or other forms of memory, highlighting the need for further research in more realistic contexts and with clinical populations. Future studies in these areas will be crucial for developing strategies to effectively address or mitigate the impact of traumatic memories, thereby enhancing the practical relevance and clinical utility of memory research. Methodological limitations inherent to fMRI's temporal resolution preclude definitive conclusions about the precise timing of neural engagement (e.g., OFG in encoding totally noval information vs. recombination phases); future temporal dissection using multimodal approaches may clarify these dynamics.

In summary, the research has illuminated the mechanisms by which enhanced memory expression with robust executive and conflict control finely preserve the original memory, while restricted memory reactivation may serve as a prerequisite for memory alteration. Meanwhile, intense processing in the visual cortex following retrieval is essential for altering the initial memory. These outcomes provide subtle yet significant evidence for the process of updating memories and impart insights relevant to clinical practice. Capitalizing on the understanding of these complex patterns enables a deeper appreciation of the intricate relationship between perception, memory, and neural adaptability. It paves the way for the development of more efficacious methodologies aimed at improving memory modification and rehabilitating biased memory functions.

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Data availability

On reasonable request, the corresponding author will provide access to the data utilized in the current work.

Ethics declarations

Ethics approval and consent to participate

All procedures performed in the study involving human participants were in accordance with the ethical standards of the institutional and national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. All experimental protocols were approved by the ethics committee of the Institute of Psychology at the Chinese Academy of Sciences (IPCAS2020004). Informed consent was obtained from all individual participants included in the study. The research team placed a high emphasis on ensuring participant privacy and confidentiality, ensuring that all obtained data was exclusively utilized for research objectives.

Consent for publication

Not applicable.

Data and code availability statement

The data and code utilized in this study will be made available upon reasonable request to the corresponding author.

CRediT authorship contribution statement

Dong-ni Pan: Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **CuiZhu Lin:** Software, Investigation, Data curation. **Ma Xin:** Software, Investigation, Data curation. **Oliver T. Wolf:** Writing – review & editing, Software, Resources, Funding acquisition, Conceptualization. **Gui Xue:** Writing – review & editing, Resources, Methodology. **Xuebing Li:** Writing – review & editing, Validation, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no conflicts of interest.

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