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Targeted stimulation of face-selective visual cortex at retrieval boosts associative face memory in healthy young adults

Hendrik Heinbockel¹, Aidan J. Horner^{2,3}, Lars Schwabe¹

¹Department of Cognitive Psychology, Universität Hamburg, Hamburg, Germany

²Department of Psychology, University of York, UK

³York Biomedical Research Institute, University of York, UK

Corresponding author:

Lars Schwabe, Department of Cognitive Psychology, Institute of Psychology, University of Hamburg, Von-Melle-Park 5, Hamburg 20146, Germany, email: Lars.Schwabe@uni-hamburg.de.

Running Title: Face-selective visual cortex stimulation enhances associative face memory

ABSTRACT

Episodic memory retrieval relies on encoding–pattern reinstatement (EPR), the reactivation of neural representations formed during encoding. Although EPR has been associated with successful remembering, it remains unclear whether this process can be proactively enhanced at retrieval. Specifically, it is unknown whether targeted brain stimulation immediately before retrieval can strengthen cortical reinstatement and improve memory in a content-specific manner. To address this question, we combined noninvasive brain stimulation with EEG in a two-day associative memory paradigm. On Day 1, participants encoded word–face and word–scene pairs. On Day 2, immediately prior to retrieval, they received either intermittent theta burst stimulation (iTBS) or sham stimulation targeted to the right occipital face area, a region specialized for face processing. Pre-retrieval iTBS selectively enhanced associative memory for faces, but not scenes. While the behavioral findings demonstrate a category-specific enhancement of memory following stimulation, the exploratory MVPA analyses on EEG data remained inconclusive as to whether EPR represents the mechanism underlying the observed memory benefit. Together, these findings show that targeted stimulation of face-selective visual cortex can selectively enhance associative face memory at retrieval, supporting a core tenet of the EPR framework and offering a potential pathway for targeted brain stimulation to alleviate content-specific memory deficits.

Keywords: Associative Memory, TMS, Theta Burst Stimulation, Visual Cortex

INTRODUCTION

Episodic memory enables individuals to consciously re-experience past events by retrieving information rich in contextual and sensory detail (Conway, 2009; Tulving, 2002). This ability is fundamental for adaptive behavior, supporting flexible decision-making, problem-solving, and the mental simulation of future scenarios (Schacter et al., 2007; Shohamy & Daw, 2015). A widely accepted theoretical framework proposes that successful retrieval depends on the reinstatement of neural activity patterns present during encoding—a process thought to re-engage the perceptual and associative circuits originally involved (Chen et al., 2017; Rugg & Vilberg, 2013). While this encoding–pattern reinstatement (EPR) model has become central to theories of episodic memory (Johnson & Rugg, 2007; Kuhl & Chun, 2014; Rissman & Wagner, 2012), its empirical foundation is mainly based on correlational evidence from neuroimaging studies (Gordon et al., 2014; Tompary et al., 2016; X. Xiao et al., 2017), and it remains unclear whether such reactivation can be selectively modulated to improve memory performance.

Current models of episodic memory emphasize the role of hippocampal–neocortical interactions in retrieval (Eichenbaum et al., 2007; Yonelinas, 2013), with the hippocampus thought to coordinate the reactivation of distributed, content-specific cortical representations (Barnett et al., 2021; Hebscher et al., 2021; Horner et al., 2015; Horner & Doeller, 2017; Staresina et al., 2012). Sensory-selective regions such as the occipital face area (OFA) are consistently engaged during both encoding and retrieval of faces, suggesting they may support content-specific reinstatement (Bracci et al., 2017; Epstein et al., 1999; Grill-Spector & Weiner, 2014; Kanwisher et al., 1997). Yet whether these areas are functionally necessary for successful retrieval remains unclear. If such regions actively support memory reactivation rather than merely reflect it, then modulating their excitability at retrieval should selectively influence

memory for their preferred content. Although this prediction has not been directly tested, addressing it would critically evaluate a core tenet of the EPR framework and reveal whether retrieval-phase neuromodulation can serve as a mechanism for targeted memory enhancement.

Noninvasive brain stimulation techniques, such as repetitive transcranial magnetic stimulation (rTMS), provide a promising tool for this purpose (Hermiller et al., 2020; Nilakantan et al., 2017; Wang et al., 2014). Intermittent theta burst stimulation (iTBS), in particular, has been shown to transiently boost cortical excitability (Huang et al., 2005). However, nearly all prior work has focused on stimulation during encoding or on general, content-unspecific, memory outcomes (Ezzyat et al., 2018; ; Nilakantan et al., 2017; Wang et al., 2014). Whether neuromodulation of category-selective regions prior to retrieval can enhance content-specific reinstatement and memory remains unknown. This represents both a conceptual and methodological gap. Targeting sensory-specific visual areas such as the OFA offers a novel and theoretically powerful approach to test whether episodic memory can be boosted by modulating the neural mechanisms of reinstatement at the point of recall. Such an approach also opens new possibilities for precision interventions in domain-specific memory deficits, such as impaired face memory in acquired prosopagnosia or semantic dementia (Greene & Hodges, 1996; Henke et al., 1998; Rivest et al., 2009; Yadollahikholes et al., 2024).

In the current study, we employed a two-day associative memory design in combination with electroencephalography (EEG) and MRI-informed ('neuro-navigated') TMS to test whether the stimulation of a face-selective visual area at retrieval can boost face-specific retrieval processes. On Day 1, participants encoded pairs of words associated with either face or scene images. On Day 2, prior to a cued recall task, participants received either iTBS targeting the rOFA or sham stimulation in a double-blind manner. We hypothesized that iTBS would

selectively enhance both behavioral memory performance and neural reactivation for face-related associations. To test this, we applied multivariate pattern analysis (MVPA) to electroencephalography (EEG) data recorded during both encoding and retrieval phases.

METHODS

Participants

Forty right-handed healthy young adults (20 males, 20 females; mean age = 24.9 years, SD = 3.3) with normal or corrected-to-normal vision took part in this study. Prior to participation, all individuals underwent a standardized screening interview to rule out exclusion criteria, including a history of neurological or psychiatric disorders, current medication or substance abuse, cardiovascular, thyroid, or renal conditions, current COVID-19 infection or exposure, and any contraindications for MRI or TMS. Participants with a body mass index (BMI) below 19 or above 26 kg/m² were also excluded. Written informed consent was obtained from all participants, who received monetary compensation upon completing the study. The experimental protocol was approved by the Ethics Committee of the Faculty of Psychology and Human Movement Science at the University of Hamburg and complied with the Declaration of Helsinki. An a priori power analysis was conducted using G*Power (Faul et al., 2007) for the primary group $\times$ category interaction in a mixed design with one within-subject factor (category: faces vs. scenes) and one between-subjects factor (stimulation group: iTBS vs. sham). Because no directly comparable studies combining the present stimulation protocol and experimental design were available, the analysis was based on an assumed medium effect size ($f = 0.25$), informed by related stimulation studies employing group $\times$ stimulus-category interactions (Abend et al., 2019; Manuel et al., 2019). The analysis indicated that a minimum sample size of

N = 38 would be required to achieve 85% power to detect the predicted interaction effect.

Participants were pseudo-randomly assigned to either the iTBS group (n = 20; 10 females) or the sham group (n = 20; 10 females), ensuring balanced gender distribution across conditions.

Experimental design

Participants completed a two-day experimental paradigm combining paired-associate learning with noninvasive brain stimulation and EEG recording. On both days, 64-channel EEG was recorded to later employ MVPA to assess EPR by classifying neural activity patterns from Day 1 Encoding and Day 2 Retrieval. The experiment was designed to examine whether targeted visual cortex stimulation could causally enhance memory reactivation and performance in a category-specific manner (faces vs. scenes).

On Day 1, participants completed two runs ($\sim 2 \times 15$ minutes) of 80 semantically unrelated word–picture pairs, each consisting of a neutral German noun and either a greyscale face or scene image (40 per category). The words were selected from the Leipzig Affective Norms for German database (Kanske & Kotz, 2010). The pictures consisted of neutral outdoor scenes from the SUN database (J. Xiao et al., 2010) and neutral faces from the CFD database (Ma et al., 2015). Each trial began with a 500 ms fixation cross, followed by a 2-second presentation of an image. After a 2-second delay, a word (coloured in red) was superimposed on the same image for 4 seconds (Figure 1A). Participants were instructed to perform a size-judgment task: using a button press, they indicated whether the object named by the word would fit inside a shoebox. This task was designed to promote incidental deep encoding. A 2-second inter-trial interval with a fixation dot followed each trial. After encoding, participants completed a recognition task including all previously presented images from the encoding task, and 40

novel images (foils; 20 scenes and 20 faces). Each trial began with a 4-second image presentation (either old or new), followed by a screen asking the participant to classify the image as “old” or “new” and, if old, to type in the associated word.

On the second day of the experiment, participants received either iTBS targeting the rOFA or sham stimulation, depending on their group assignment. Following stimulation, participants completed a cued recall test. Each trial consisted of the presentation of a single word—either previously studied on Day 1 or a novel lure—for 2 seconds. Participants were instructed to mentally visualize the image (scene or face) they had associated with the word during encoding. Within a 4-second response window, participants completed a four-alternative forced-choice (4AFC) task by selecting one of the following response options: “new”, “old”, “old/scene”, or “old/face”. Participants were instructed to respond “old” if they recognized the cue word as previously studied but could not retrieve either the associated picture or its category. The responses “old/scene” and “old/face” were to be selected only when both the word was recognized as old and the associated picture category could be retrieved.

T1 MR Image Acquisition and Neuronavigation

Before the experimental session, we obtained individual T1-weighted structural MR images using a 3T Siemens PRISMA scanner from each participant. These images were used for neuro-navigation with the PowerMag View! System (MAG & More GmbH, München, Germany). The system utilizes two infrared cameras (Polaris Spectra) to track the positions of the participant’s head and TMS coil in space. Based on the individual T1 MR images, we created 3D reconstructions of the participants' heads, allowing us to precisely locate the right occipital face area coordinate (MNI: 38, -70, -6; Ganel et al., 2005; Kadosh et al., 2011; Pitcher et al.,

2011) for TMS stimulation. Once the coordinate was entered, the coil was positioned in accordance with the template provided by the neuro-navigation system, aiming for a brain-to-target distance of less than 3 cm. This procedure ensured precise coil placement tailored to the unique anatomy of each participant, while maintaining the shortest and therefore optimal distance to the cortex.

‘Neuro-navigated’ Transcranial Magnetic Stimulation

On Day 2, participants received iTBS targeting the rOFA, or sham stimulation, prior to completing the cued recall task. To determine the stimulation intensity, individual resting motor thresholds were assessed while participants were seated at rest, wearing an EEG cap (without electrodes attached). Surface electromyography (EMG) was recorded from the right abductor pollicis (APB) brevis muscle using disposable Ag/AgCl electrodes, with the reference electrode placed on the index finger and the ground electrode on the right elbow. To identify the motor hotspot over the left primary motor cortex, we used a 9-point grid (1 cm spacing) centered approximately 5 cm left and 3.5 cm anterior to the vertex, oriented at a 45° angle. Single TMS pulses were delivered starting at 40% of the maximum stimulator output (MSO), increasing in 5% increments until reliable motor-evoked potentials (MEPs) were observed. The motor hotspot was defined as the location where stimulation consistently elicited MEPs in the APB. The resting motor threshold was defined as the minimum stimulator intensity (% MSO) required to elicit MEPs with a peak-to-peak amplitude of at least 50 μ V in at least 8 out of 16 consecutive pulses. This threshold served as the basis for calculating stimulation intensity used in the iTBS protocol (80% of the participant’s resting MT). On average, stimulation in the iTBS group was applied with an intensity of 50.1 ($\pm$ 5.0 SD %). A high-resolution T1-weighted anatomical scan had been

acquired for all participants in a prior session. These individual structural images were used to guide TMS coil placement via neuronavigation using an infrared camera system (PowerMAG View!). The rOFA target site was identified on each participant's T1 image and marked in the neuronavigation software. During stimulation, coil positioning was continuously monitored to ensure accurate and consistent targeting of the predefined anatomical site.

Stimulation was administered using a PowerMAG Research 100 stimulator (MAG & More GmbH, Munich, Germany), a device specifically designed for repetitive TMS (rTMS) in both clinical and research settings. Depending on the experimental condition, participants received either iTBS or sham stimulation. For the active stimulation condition, we used the PMD70-pCool figure-of-eight coil, which delivers a maximum magnetic field strength of 2 Tesla. For the sham condition, we employed the PMD70-pCool-SHAM coil, which is visually identical to the active coil but generates only a minimal magnetic field that does not penetrate the skull. This coil is designed to mimic the sensory experience of active stimulation by delivering surface-level pulses to the scalp, without inducing cortical activation. Both coils were 70 mm in diameter and attached to a mechanical holder to ensure a stable and tangential position on the scalp, with the coil handle pointing upward. Throughout stimulation, neuronavigation was used to maintain consistent targeting of the rOFA and to ensure that the coil-to-brain distance remained below 6 cm from the individualized stimulation coordinate. The iTBS protocol followed the standard stimulation pattern (Huang et al., 2005) consisting of 600 pulses delivered in 20 trains of 10 bursts each. Each burst comprised 3 pulses at 50 Hz, delivered every 200 ms (5 Hz), with 8-second inter-train intervals, resulting in a total stimulation duration of 3 minutes and 47 seconds. The experiment was conducted in a double-blind manner: neither participants nor experimenters were aware of the stimulation condition (iTBS vs. sham), as the different coils

looked exactly the same and produced the same kind of noise. The coil setup and stimulation was conducted by a separate experimenter. Both, participants and the experimenter were asked to guess the stimulation condition following completion of the experiment in order to assess the effectiveness of the double-blind procedure. The experimenter correctly guessed the active stimulation condition in 35.0% of cases and the sham condition in 50.0% of cases. Participants correctly identified the active stimulation condition in 50.0% of cases and the sham condition in 55.0% of cases. Overall, these values were close to chance level, suggesting that neither participants nor the experimenter were able to reliably distinguish active from sham stimulation and supporting the effectiveness of the blinding procedure.

Electric Field Simulations

Individual electric field simulations were performed using SimNIBS 4.0 with the CHARM head-modeling pipeline. For each participant, a subject-specific tetrahedral head model was generated from the individual T1-weighted MRI using CHARM with automatic tissue segmentation and mesh generation. TMS simulations were conducted using a Magstim 70-mm figure-of-eight coil. Individual stimulation intensities were incorporated by converting the applied stimulator output to the corresponding coil current rate of change (dI/dt), assuming a maximum dI/dt of 1.0×10^8 A/s. In addition, individually measured coil-to-scalp distances were specified for each participant to account for differences in coil positioning. Electric field simulations were performed for each participant using the individualized head model and stimulation parameters. To quantify stimulation strength at the target site, the group-level target coordinate in the right occipital face area (MNI: 38, -70, -6) was transformed into each participant's native anatomical space. A spherical region of interest (10-mm radius) centered on

the transformed target coordinate was defined within gray matter, and the electric field magnitude ($|E|$) was extracted from all gray matter elements within this region. The primary measure of stimulation strength was the 99th percentile of the electric field magnitude (E_{99} , V/m), which provides a robust estimate of peak stimulation while reducing the influence of numerical outliers.

EEG Data Acquisition and Preprocessing

Continuous EEG data were recorded on both experimental days using a 64-channel BioSemi ActiveTwo system (BioSemi B.V., Amsterdam, The Netherlands), with electrodes positioned according to the international 10–20 system. The data were sampled at 1024 Hz, with an online band-pass filter of 0.03–100 Hz applied during acquisition. Additional electrodes were placed on the mastoids, above and below the right eye, and at the outer canthi to monitor ocular and muscle artifacts. Electrode impedance was controlled via BioSemi's common mode sense (CMS) and driven right leg (DRL) electrodes, which served as active reference and ground, respectively, ensuring signal quality within a $\pm 20 \mu\text{V}$ range.

Offline preprocessing of the EEG data was conducted using the FieldTrip toolbox (Version 20200607; Oostenveld et al., 2011) in MATLAB (Version 2019a, The MathWorks, Inc.) along with custom scripts. EEG data were segmented into epochs from -2 to +10 seconds relative to stimulus onset (first image during encoding on Day 1, and word cue during retrieval on Day 2). Signals were re-referenced to the average of all scalp electrodes, demeaned based on the average signal within each trial, and linearly detrended. To remove line noise, a 50 Hz discrete Fourier transform filter was applied. Electrodes showing no signal or excessive noise (limited to a maximum of one per participant) were excluded and interpolated using weighted

neighboring electrodes. Trials with gross artifacts were removed based on visual inspection. On Day 1, on average 7 trials (SD = 5.37) out of 160 were excluded per participant. On Day 2, on average 9 trials (SD = 7.29) out of 160 were excluded per participant. To ensure that subsequent MVPA was trained and tested on corresponding data, any Day 1 (encoding) trials removed due to artifacts were also excluded from the Day 2 (retrieval) dataset, and vice versa. This trial-matching procedure ensured that classification analyses were performed only on trials with usable data from both encoding and retrieval phases. Following artifact rejection, data were downsampled to 256 Hz to reduce computational load. Next, an extended infomax independent component analysis (ICA) was performed using the ‘runica’ algorithm, with a stopping criterion set to a weight change of $<10^{-7}$. This was used to identify and remove components reflecting ocular artifacts and other stereotyped noise sources. A two-step procedure was applied: first, the time series of each independent component was correlated with horizontal and vertical EOG signals. Components showing a correlation > 0.9 were automatically rejected. Remaining components were then manually reviewed based on their time course and spatial topography. On average, 2.27 components (SD = 1.01) per participant were removed via this process.

Encoding-Pattern-Reinstatement Analysis

For the explorative multivariate decoding analysis, EEG data from the encoding and cued recall tasks were segmented into 2.5-second epochs. For the encoding phase, epochs covered (i) the encoding interval (during initial image presentation, without the word) as well as (ii) the post-encoding rest interval (after initial image presentation, without the word), and were baseline-corrected using the 500 ms window preceding fixation cross onset. For the cued recall phase, epochs spanned the presentation of the cue word and were baseline-corrected using the

500 ms interval before word onset. To reduce computational load and memory requirements associated with the large time $\times$ time decoding matrices, classifier outputs were spatially downsampled using a 3×3 averaging kernel prior to statistical analysis. We employed two L2-penalized logistic regression classifiers, using data from all EEG channels as input features.

The first classifier was trained and tested within the stimulus presentation period data (during image presentation, without the word), using a 5-fold cross-validation procedure to assess whether neural activity patterns could reliably distinguish between faces and scenes. This analysis aimed to probe category-specific encoding and processing during image presentation. The second classifier was trained and tested within the post-stimulus presentation period data (after initial image presentation, without the word), using a 5-fold cross-validation procedure to assess whether neural activity patterns could reliably distinguish between faces and scenes. This analysis aimed to probe category-specific encoding and processing immediately following image presentation. The resulting time-by-time decoding accuracy matrices captured the strength and temporal dynamics of this category-specific neural differentiation during the post-encoding interval.

The third model explored whether category-specific encoding patterns would be reactivated during successful retrieval. To this end, the classifier was trained within-subject on the stimulus presentation data to distinguish between scene and face trials. This trained model was then tested on the cued recall data to decode neural patterns during cue word presentation on Day 2. The fourth model explored whether category-specific post-encoding patterns would be reactivated during successful retrieval. To this end, the classifier was trained within-subject on the post-stimulus presentation data to distinguish between scene and face trials. This trained model was then tested on the cued recall data to decode neural patterns during cue word

presentation on Day 2. For both models, trial-wise time-by-time category reinstatement evidence was assessed using logits, which represent the signed distance of each sample to the separating hyperplane between scenes and objects.

Statistical analysis

In our analysis of word-picture associative memory for the cued recall tasks on Day 2 (4AFC), associative category hits were defined as trials in which old word cues were presented and participants responded with the correct picture category (e.g. “old/face” when the associate had been a face), indicating the recognition of the presented word as old and category-level retrieval of the associated picture category. Associative category errors included all trials in which an old word was recognized, but the wrong category was chosen (e.g., “old/scene” when the associate had been a face). For our behavioral analyses, we employed a generalized linear mixed-effects model (GLMM), given its robustness to violations of distributional assumptions and its sensitivity to individual variability (Pinheiro & Bates, 2000; Schielzeth et al., 2020). To examine the effects of iTBS on associative memory performance, we focused on associative hits (i.e., correctly choosing “old/scene” or “old/face” during cued recall) and associative errors (i.e., incorrectly choosing “old/scene” when the word had been paired with a face on Day 1). A GLMM was fitted using the lme4 package in R version 4.0.4 (Bates et al., 2015), including group (iTBS vs. sham), category (scene vs. face), their interaction as fixed effects, a random intercept per participant as well as category as a random slope for the participant intercept. All models were evaluated using standardized beta coefficients. Prior to analysis, data were screened for outliers, defined as values exceeding ± 3 standard deviations from the mean. All reported p-

values from statistical models and post-hoc tests reported throughout the manuscript were corrected for multiple comparisons with Bonferroni correction (for number of tests).

To assess decoding results, category-specific classification accuracy (faces vs. scenes) across time $\times$ time-decoding-matrices was first assessed using a within-subject cluster-based permutation t-test (10,000 permutations; Maris & Oostenveld, 2007). This test compared scene versus face reinstatement maps within each group (iTBS, sham) to identify clusters of time points showing significant differentiation. We then computed within-subject difference maps (faces – scenes) and subjected these to an independent-samples cluster-based permutation t-test (10,000 permutations) to assess differences in category-specific reinstatement between the iTBS and sham groups. This nonparametric approach controlled for multiple comparisons across time without imposing spatial or temporal constraints. Clustering was performed at a threshold of $\alpha_{\text{cluster}} = 0.01$ (for testing EPR across groups $\alpha_{\text{cluster}} = 0.001$), and clusters with corrected Monte Carlo p-values < 0.05 (two-sided) were considered statistically significant.

RESULTS

Day 1: Successful Memory Encoding

On Day 1, participants encoded 80 semantically unrelated word–picture pairs (40 faces, 40 scenes) across two runs. In a recognition task, immediately after encoding, participants were presented with all previously studied (“old”) images, as well as 40 new images (Fig. 1A). Within four seconds, participants were requested to select one out of two response options: “new” or “old” on each trial (2AFC decision). Participants correctly recognized old images in 83.9% (± 2.13 SE) of the trials, with a false alarm rate of 4.18% (± 0.97 SE). Importantly, image recognition

performance did not differ between stimulus categories (faces, scenes), nor between participants that would receive iTBS vs. sham stimulation on Day 2 (all main effect and interaction P s > 0.409). Upon successful image recognition, participants were asked to type in the associated word. Participants correctly entered the associated words in 34.8 % of the trials (± 2.88 SE). Across groups, word retrieval performance did not differ between word-scene and word-face associations (Main effect category: $F(1,74) = 3.732$, $P = 0.057$). Importantly, word retrieval performance did not differ between groups (group main effect and group interaction P s > 0.349). Overall, these results suggest robust and similar word-picture pair acquisition across groups.

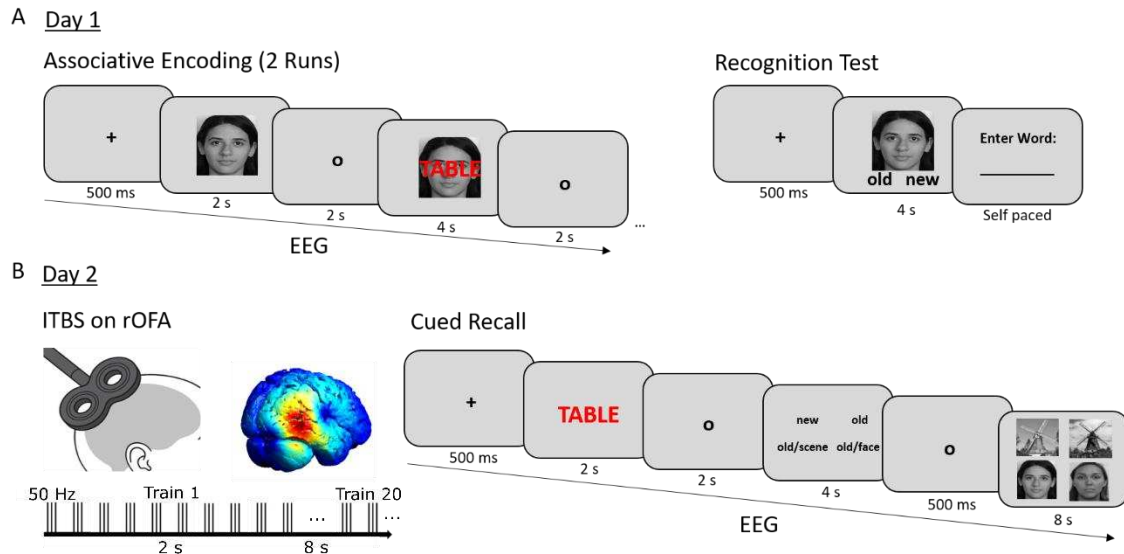


Figure 1. Overview of experimental procedure across days. **A** On Day 1, participants encoded 80 semantically unrelated word–picture pairs (40 faces, 40 scenes) across two ~15-minute runs. Each pair consisted of a neutral German noun and a greyscale image—either a face or an outdoor scene. Each trial began with a 500 ms fixation, a 2-second image, followed by a 2-second delay and a 4-second word–image overlay. After encoding, participants completed a recognition test with all studied images and 40 foils. For each trial, they judged whether the image was “old” or “new” and, if old, typed in the associated word. **B** On Day 2, 24 h after encoding, participants received either intermittent theta burst stimulation (iTBS) targeting the right occipital face area (rOFA) or sham stimulation. Magnetic Field simulations confirmed successful iTBS stimulation, with all iTBS participants showing robust electric field induction on the group level. Following (sham-) stimulation, they completed a cued recall task. Each trial presented a word (old or lure) for 2 seconds, prompting participants to mentally visualize and recall the associated image. Within 4 seconds, they classified the word as “new,” “old,” “old/scene,” or “old/face” (4AFC). Finally, they completed a cued recall task by selecting the correct image from two face and two scene options. Notably, this Day 2 memory test differed from the one on Day 1 by presenting the word cue first and asking for the associated image.

Day 2: iTBS on rOFA enhances subsequent associative memory retrieval for faces

On Day 2, 24 hours after the encoding session, participants received either iTBS or sham stimulation over the rOFA (between-subjects design). Magnetic Field simulations confirmed successful iTBS stimulation, with all iTBS participants showing robust electric field induction (t-test against 0: $t(19) = 5.54$, $P < 0.001$, $d = 1.23$; Figure 1B *left*). Immediately afterward, they completed a cued recall task to assess the effect of stimulation on associative memory performance (4AFC; Fig. 1B). In each trial, a word cue (previously encoded or novel) was presented for 2 seconds. Within a 4-second response window, they selected one of four options: “new”, “old”, “old/scene” or “old/face”. Participants were instructed to press the “old” option if they recognized a word but could not remember whether it was paired with a face or scene. Overall, participants correctly recognized old words in 90.2% (± 1.32 SE) of the trials (responses “old”, “old/scene”, and “old/face” to old word cues), with a false alarm rate of 15.24 % (± 1.49 SE; responses “old”, “old/scene”, and “old/face” to new word cues). Importantly, overall word recognition did not differ between the iTBS and sham group ($P = 0.462$).

In line with our main hypothesis, iTBS over the face-selective rOFA enhanced associative memory selectively for pairs including face stimuli. We analyzed participants’ performance in the cued recall task where they had to recognize whether a word was paired with a face or a scene 24 hours before. Across groups, an associative hit rate of 59.1 % (± 3.59 SE) was observed. Using a generalized linear mixed-effects model (GLMM), we examined how often participants correctly identified the category (face vs. scene) associated with each word (associative hits) versus how often they made errors by choosing the wrong category (associative errors). We found a significant interaction between the stimulation group (iTBS vs. sham) and stimulus category (faces vs. scenes), indicating that the iTBS group had a significant memory

improvement for faces compared to scenes ($\beta = 0.84$, $P = 0.004$; Fig. 2). Post-hoc comparisons revealed that participants who received active iTBS to the rOFA had a significantly higher predicted probability of recalling faces compared to scenes ($\beta = 2.46$, $P_{\text{corr}} < 0.001$; Bonferroni-corrected for two comparisons within the stimulus category $\times$ stimulation interaction), confirming a category-specific memory boost. Importantly, this effect was absent in the sham group, where no significant difference between face and scene memory performance was found ($\beta = 1.11$, $P_{\text{corr}} = 0.771$; Bonferroni-corrected for two comparisons within the stimulus category $\times$ stimulation interaction). To rule out that the observed memory effect was based on an induced response bias towards face stimuli, we compared the associative error rates of the Day 2 Cued Recall across groups and categories. Importantly no group $\times$ category interaction on associative errors was detected ($P = 0.632$). Together these results indicate that the enhanced associative face memory was specifically due to stimulation of the rOFA, rather than a general improvement, response bias or placebo effect. Table 1 reports the complete distribution of responses, including both correct and incorrect response categories, separately for stimulation group and stimulus category. Importantly, the iTBS group did not exhibit an increased tendency to select face-related responses when incorrect. These response patterns support the conclusion that the observed stimulation effect reflects enhanced associative retrieval for face-word pairs rather than a category-specific response bias.

Table 1 Response distribution for the Cued Recall on Day 2

Response	New words		Old words paired with face		Old words paired with face	
	iTBS	Sham	iTBS	Sham	iTBS	Sham
New	69.1 (1.60)	66.5 (1.76)	3.11 (0.43)	5.83 (1.14)	2.31 (0.32)	4.94 (0.74)
Old	8.2 (1.14)	7.77 (0.97)	12.23 (2.06)	9.47 (1.64)	12.29 (2.0)	8.83 (1.68)
Old_scene	1.5 (0.15)	4.30 (0.97)	2.42 (0.33)	4.93 (1.04)	23.6 (2.20)	23.45 (2.16)
Old_face	2.64 (0.65)	4.14 (0.67)	24.85 (2.30)	22.65 (1.82)	4.8 (1.08)	6 (1.06)

Data reflect Mean $\pm$ SE.

Following each 4AFC decision, participants proceeded to an image recognition task (if they selected one of the “old” response options). Here, they were presented with two face images and two scene images and were asked to choose the one that corresponded to the word presented in that trial. Average performance in this recognition test revealed however near ceiling effects of correct image recognitions ($M = 88.6\%$, $SE = \pm 2.10\%$), with no category $\times$ group interaction ($P = 0.411$).

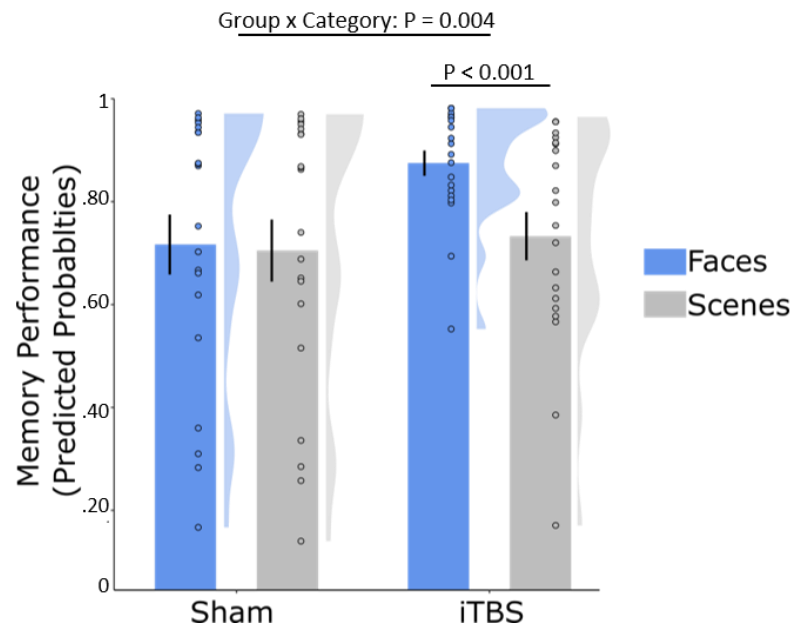


Figure 2. Category-specific associative memory enhancement following iTBS over the rOFA. Predicted probabilities of correct associative memory (associative hits) for face- and scene-paired words in the cued recall task on Day 2, plotted separately for the iTBS and sham groups. A GLMM revealed a significant interaction between stimulation group and stimulus category, with active iTBS selectively improving memory for word-face associations compared to word-scene associations. Post-hoc comparisons confirmed that this face-specific enhancement was present only in the iTBS group and not in the sham group. Error bars represent ± 1 SE.

To assess whether variability in stimulation delivery contributed to memory performance, we conducted a generalized linear mixed-effects analysis within the iTBS group. The model included stimulus category (faces vs. scenes) and estimated electric field strength (note that the individual coil-to-target distance was already included in the electric field simulations), and their interactions as fixed effects. Estimated electric field strength ($P = .185$) did not predict associative memory performance, and also did not interact with stimulus category ($P = .079$), indicating that the category-specific memory enhancement observed following iTBS could not be explained by individual differences in stimulation intensity. Notably, coil-to-target distance was comparable between groups (iTBS: 3.01 ± 0.20 cm; sham: 2.85 ± 0.19 cm), suggesting similar stimulation quality across conditions.

Day 2: Exploratory analysis of encoding–pattern reinstatement during successful associative retrieval of faces following pre-retrieval iTBS over the rOFA

Our behavioral results provide strong evidence that iTBS over the rOFA prior to retrieval selectively improves associative memory for faces but not scenes, demonstrating a content-specific memory enhancement effect. In a next step, we explored potential neural mechanisms underlying this behavioral benefit using multivariate pattern analysis (MVPA) of the EEG data.

First, we trained and tested classifiers to distinguish neural face patterns from scene patterns within the Day 1 encoding data using a 5-fold cross-validation procedure. Separate models were trained on activity during stimulus presentation and during the post-stimulus period. Dependent-sample cluster-based permutation t-tests against chance level (0.5) revealed one significant cluster ranging from 0.1 to 0.3 s after stimulus onset ($P < 0.001$, $T_{\text{sum}} = 1022.51$)

during stimulus presentation. For the post-encoding model, dependent-sample cluster-based permutation t-tests against chance level (0.5) revealed two significant clusters in both analyses, confirming that neural activity reliably differentiated faces from scenes during encoding (Early Cluster: 0.1–0.7 s from stimulus onset, $P < 0.001$, $T_{\text{sum}} = 1790.81$; Late Cluster: 0.9–1.75 s from stimulus onset, $P = 0.001$, $T_{\text{sum}} = 1388.88$). These findings demonstrate robust category-specific neural representations during and shortly after encoding.

Next, we conducted exploratory analyses of encoding–retrieval pattern reinstatement (EPR) during successful retrieval. For these analyses, classifiers trained to distinguish face and scene representations during Day 1 encoding were tested on Day 2 EEG data recorded during the word-cue period of successful associative retrieval trials. The resulting time $\times$ time reinstatement matrices quantified the reactivation of category-specific encoding patterns during retrieval. Before testing for stimulation effects, we first examined encoding–retrieval pattern reinstatement across groups (cluster-tests against 0). Significant reinstatement was observed for both face- (Cluster: 0.2–0.7 s from stimulus onset, $P < 0.001$, $T_{\text{sum}} = 6368.90$) and scene-associated memories (Cluster: 0.25–0.6 s from stimulus onset, $P < 0.001$, $T_{\text{sum}} = 4533.61$), indicating that the decoding approach successfully captured EPR at the group level. To examine whether the behavioral effects of stimulation were accompanied by changes in reinstatement, we compared face-versus-scene reinstatement differences between the iTBS and sham groups using independent-sample cluster-based permutation t-tests. Neither the stimulus-presentation (all channels: all cluster P s > 0.360 ; parietal: no significant clusters; occipital: no significant clusters; frontal: all cluster P s > 0.348 ; central: all cluster P s > 0.296 ; temporal: no significant clusters) nor the post-stimulus model (all channels: all cluster P s > 0.377 ; parietal: all cluster P s > 0.079 ; occipital: all cluster P s > 0.121 ; frontal: all cluster P s > 0.369 ; central: all cluster P s $>$

0.530; temporal: all cluster P s > 0.210) revealed a significant difference in reinstatement between faces and scenes in the iTBS.. Thus, although iTBS selectively enhanced associative memory for faces, the exploratory MVPA analyses did not provide evidence that stimulation modulated encoding–retrieval pattern reinstatement. Together, these findings suggest that the observed behavioral benefit cannot be readily explained by enhanced EPR.

DISCUSSION

The present study combined noninvasive brain stimulation, EEG-based multivariate pattern analysis, and a two-day associative memory paradigm to test whether targeted modulation of a face-selective cortical region can enhance associative face memory. Crucially, stimulation was applied immediately prior to retrieval, allowing us to directly manipulate neocortical reinstatement at retrieval without altering encoding. Behaviorally, iTBS to the rOFA selectively improved associative memory for faces, with no effect on associative scene memory. By showing that focal neuromodulation can selectively enhance associative face memory via retrieval-targeted stimulation, our findings advance theories of episodic memory and suggest a novel, translationally relevant approach to treating domain-specific memory deficits such as semantic dementia or acquired prosopagnosia.

Our behavioral findings demonstrate a robust category-specific enhancement of associative memory following iTBS to the rOFA. Specifically, participants who received iTBS before retrieval showed significantly improved recall for word-face pairs compared to word-scene pairs, an effect absent in the sham group. This finding shows that modulating neural excitability in face-selective visual cortex can selectively facilitate the retrieval of face-related episodic associations. These results significantly extend prior neuroimaging studies that have

shown increased functional connectivity between the hippocampus and category-selective regions (such as the FFA and OFA) during associative memory tasks (Nilakantan et al., 2017; Staresina et al., 2013; Wang et al., 2014), by providing causal evidence that directly stimulating these sensory regions at retrieval can enhance associative memory performance. Moreover, our findings resonate with reports that disrupting activity in the OFA using inhibitory TMS can impair face processing (Bona et al., 2018; Eick et al., 2021; Pitcher et al., 2007), but importantly extend these data to the domain of associative memory reinstatement and move beyond disruption to show that facilitative stimulation can improve memory outcomes in a category-specific manner.

To explore the neural mechanisms underlying this behavioral benefit, we conducted exploratory MVPA analyses of EEG data recorded during encoding and retrieval. Consistent with previous work, classifiers reliably distinguished face-related from scene-related neural activity during encoding, confirming the presence of robust category-specific neural representations (Cauchoix et al., 2014; Grootswagers et al., 2017, 2019). However, contrary to our expectations, the exploratory reinstatement analyses did not reveal evidence that iTBS modulated encoding–retrieval pattern reinstatement (EPR). Although stimulation improved associative memory performance for faces, this behavioral enhancement was not accompanied by detectable changes in EEG-based reinstatement measures.

Several interpretations of this null finding are possible. First, the behavioral effects of iTBS may be mediated by neural processes that are not adequately captured by the present MVPA approach. For example, stimulation may have influenced attentional allocation, retrieval monitoring, decision-related processes, or other retrieval-related computations that contribute to successful remembering without necessarily producing measurable changes in category-level

reinstatement. Second, although the decoding approach successfully detected reinstatement overall, it remains possible that stimulation-related changes occurred at a spatial or temporal scale that could not be resolved using scalp EEG and the present MVPA framework.

Consequently, the current findings do not rule out a contribution of reinstatement to the observed memory enhancement but indicate that we found no evidence that iTBS modulated EPR as measured here.

Interestingly, our decoding analyses nevertheless revealed robust category-specific neural representations during and shortly after encoding. Neural activity reliably differentiated faces from scenes both during stimulus presentation and during subsequent post-stimulus processing periods. This finding aligns with previous work suggesting that memory-relevant neural representations extend beyond the initial perceptual response and remain active during sustained encoding-related processing (Heib et al., 2015; Khader et al., 2005; Michelmann et al., 2018; Sederberg et al., 2003). Such post-stimulus activity may reflect elaborative processing, associative binding, or early consolidation-related mechanisms that contribute to the formation of durable memory traces (Ranganath et al., 2005; Ranganath & Ritchey, 2012).

Beyond elucidating the neural underpinnings of episodic memory, our results highlight the utility of iTBS as a tool not merely for probing causal involvement of brain regions by disruption, but for actively enhancing neural processes and associated cognitive functions. While a vast range of TMS studies on episodic memory have employed protocols designed to transiently inhibit cortical activity to infer functional necessity (Eick et al., 2021; Platz et al., 2016; Vékony et al., 2018), iTBS represents a distinct approach aimed at increasing cortical excitability and plasticity (Huang et al., 2005). Here, we show that iTBS targeting face-selective visual cortex can selectively boost the fidelity of mnemonic reinstatement and thereby improve

behavioral memory outcomes. This demonstrates the promise of moving from “virtual lesion” paradigms toward protocols that can facilitate targeted neural processes and their cognitive correlates.

It is, however, important to note that although the use of a sham condition as the control is a standard and methodologically valid approach, it does not afford the same level of regional specificity as a design including an active, functionally related but dissociable control site. Hence, the present design does not allow us to fully dissociate the effects of rOFA stimulation from potential effects on other stimulus domains (e.g., scenes), as no group received iTBS to a scene-selective visual region. Moreover, evidence that the effects of offline TMS can spatially diffuse further necessitates caution when interpreting region-specific mechanisms. Consequently, the current findings cannot determine whether the observed enhancement in associative memory retrieval is uniquely attributable to modulation of face-selective cortex or reflects a more general influence of visual cortical stimulation on memory processes. Nevertheless, the effect was selective to the face-associated retrieval condition, providing converging support for the functional involvement of the targeted face-selective visual region (OFA). Future studies incorporating active control sites in other category-selective regions, such as scene-selective cortex, will be necessary to test for such dissociations and to strengthen claims regarding functional and regional specificity.

Another limitation of the present study concerns the definition of the rOFA stimulation target. Specifically, stimulation coordinates were based on a previously reported group-level MNI coordinate that was transformed into each participant’s native anatomical space. Although this procedure accounts for inter-individual variability in neuroanatomy, it does not necessarily capture variability in functional face selectivity across participants. Consequently, the stimulated

site may not have corresponded to the functionally most face-selective region in every individual. Future studies could address this limitation by combining neuronavigated stimulation with individual functional localizers to identify participant-specific rOFA regions showing maximal face responsiveness, potentially improving targeting precision and sensitivity to stimulation effects.

Taken together, our findings provide causal evidence that focal neuromodulation of face-selective visual cortex before retrieval can selectively enhance associative face memory. These results highlight the contribution of category-selective cortical regions to episodic retrieval and demonstrate that memory performance can be improved through targeted stimulation immediately prior to recall. Although exploratory EEG-MVPA analyses did not reveal corresponding changes in encoding–retrieval pattern reinstatement, the robust behavioral effects observed here establish retrieval-phase neuromodulation as a promising approach for selective memory enhancement. From a translational perspective, these results open avenues for developing targeted brain stimulation interventions to alleviate content-specific memory impairments, such as those seen in prosopagnosia or domain-specific amnesia, laying the groundwork for individualized cognitive enhancement approaches.

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Conflict of interest

The authors declare no competing financial interests related to this manuscript.

Data and Code Availability

The behavioral and raw as well as processed EEG data generated in this study have been deposited together with the code used for analyses in the Federal Data Repository of the University of Hamburg (<https://www.fdr.uni-hamburg.de/record/17815>).

CRedit authorship contribution statement

Hendrik Heinbockel: Data curation, Formal analysis, Validation, Visualization, Methodology, Writing – original draft, Writing – review and editing. **Aidan J. Horner:** Conceptualization, Validation, Writing – review and editing. **Lars Schwabe:** Conceptualization, Project administration, Resources, Supervision, Funding acquisition, Writing – original draft, Writing – review and editing.