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Spatiotemporal Neural Pattern Similarity Supports Episodic Memory

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Report

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Highlights

- EEG STPS during encoding predicted later memory
- Item-specific STPS occurred around 500 ms after stimulus onset
- LPFC anodal tDCS enhanced subsequent memory and item-specific STPS

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In Brief

Using EEG and tDCS, Lu et al. examined the neural mechanisms of memory formation. They found that greater item-specific STPS during encoding predicted better later memory. Anodal tDCS over the left LPFC specifically enhanced STPS and memory.

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Report

Spatiotemporal Neural Pattern Similarity Supports Episodic Memory

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Summary

Formal computational models of human memory posit a central role of feature representations in episodic memory encoding and retrieval [1–4]. Correspondingly, fMRI studies have found that, in addition to activity level [5, 6], the neural activation pattern similarity across repetitions (i.e., self-similarity) was greater for subsequently remembered than forgotten items [7–9]. This self-similarity has been suggested to reflect pattern reinstatement due to study-phase retrieval [7, 10, 11]. However, the low temporal resolution of fMRI measures could determine neither the temporal precision of study-phase reinstatement nor the processing stage at which the reinstatement supported subsequent memory [12]. Meanwhile, although self-similarity has been shown to correlate with the activity level in the left lateral prefrontal cortex (LPFC) [10, 13], a causal link between left LPFC function and pattern similarity remains to be established. Combining transcranial direct current stimulation (tDCS) and EEG, we found that greater spatiotemporal pattern similarity (STPS) across repetitions of the same item (i.e., self-STPS) during encoding predicted better subsequent memory. The self-STPS located in the right frontal electrodes occurred approximately 500 ms after stimulus onset, reflected item-specific encoding, and contributed to memory above and beyond the effects of ERP amplitude and global pattern similarity (i.e., similarity to all other items in memory space). Anodal stimulation over the left LPFC specifically enhanced memory performance and item-specific STPS in the right frontal electrodes. These results support a causal role of LPFC in enhancing STPS and memory and contribute to a mechanistic understanding of memory formation.

Results

Previous fMRI research has shown that neural activation pattern similarity during encoding predicted subsequent memory [7–9, 13–15]. However, due to its limited temporal resolution, fMRI data cannot pinpoint the time point during encoding when neural activation pattern similarity starts to matter. Moreover, no experimental manipulation of pattern similarity has been used to establish its causal role in subsequent memory. These issues were addressed in the current study by combining electroencephalography (EEG) and transcranial direct current stimulation (tDCS).

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We recorded EEG while 20 participants were studying the visual forms of 120 novel visual symbols (i.e., Korean Hangul characters), using a visual structure judgment task (Figure 1A). Each character was repeated three times, with an inter-repetition-interval (IRI) of 4–7 trials. Their recognition memory was probed 1 day later using a six-point old or new judgment task (Figure 1B). Participants finished two sessions of the same task (1 week apart): once after 20 min anodal tDCS over the left lateral prefrontal cortex (LPFC) and once after sham stimulation (Figure 1C). The order of the two sessions was counterbalanced across participants. We targeted the left LPFC because it has been consistently implicated in memory encoding [5, 10, 16, 17], including evidence from tDCS studies [18, 19], and because this region's activity is positively correlated with neural activation pattern similarity in the posterior regions [10, 13].

Anodal tDCS Selectively Enhanced Memory Performance

Memory performance was indexed by the hit rate and d′. Because participants finished two sessions of the task, we first confirmed that there was no significant practice effect in memory performance for either the hit rate ($t(19) = 0.16$, $p = 0.87$) or d′ ($t(19) = 0.33$, $p = 0.75$). Compared to sham stimulation, anodal tDCS over the LPFC significantly increased the number of remembered items (scored 4 and above) ($t(19) = 3.63$, $p = 0.002$) and d′ ($t(19) = 2.28$, $p = 0.03$) (Figure 1D). There was no difference in false alarm (FA) rate ($t(19) = -0.57$, $p = 0.57$). Further examination of the confidence distribution indicated that the tDCS effect on memory performance was achieved by a shift from misses to hits (Table S1), but not by an increase from low to high confidence.

We also examined behavioral performance during encoding where subjects were asked to judge the visual structure (left-right versus top-bottom) of the characters. Two-way (stimulation by repetition) ANOVA revealed no significant interaction for either reaction time ($F(2,38) = 1.15$, $p = 0.33$) or accuracy ($F(2,38) = 0.48$, $p = 0.62$). Across repetitions, the reaction time decreased ($F(2,38) = 62.86$, $p < 0.001$) and accuracy increased ($F(2,38) = 3.43$, $p = 0.043$), but tDCS did not affect the reaction time ($F(1,19) = 0.03$, $p = 0.871$) or accuracy ($F(1,19) = 0.06$, $p = 0.807$) (Figures 1E and 1F). Together, these results demonstrate that anodal tDCS selectively enhanced subsequent memory without affecting behavioral performance during encoding.

Subsequently Remembered Items Showed Greater Item-Specific STPS

We hypothesized that subsequently remembered items would show greater spatiotemporal pattern similarity (STPS) across the three repetitions (i.e., self-STPS) [7]. The self-STPS reflects the distinctiveness and reproducibility of item-specific encoding. It is calculated for single-trial EEG epochs following Kriegeskorte et al. [20] (Figure S1 and Supplemental Experimental Procedures). To improve STPS's spatial resolution, we divided the 64 electrodes into six regions (Figure 2A). Within each region, the EEG responses from all channels within 100 ms sliding windows (with a step size of one sampling point) were chosen as features. Several temporal clusters in the late time window showed greater self-STPS for remembered items than for forgotten items (Figure 2B). Two temporal clusters,

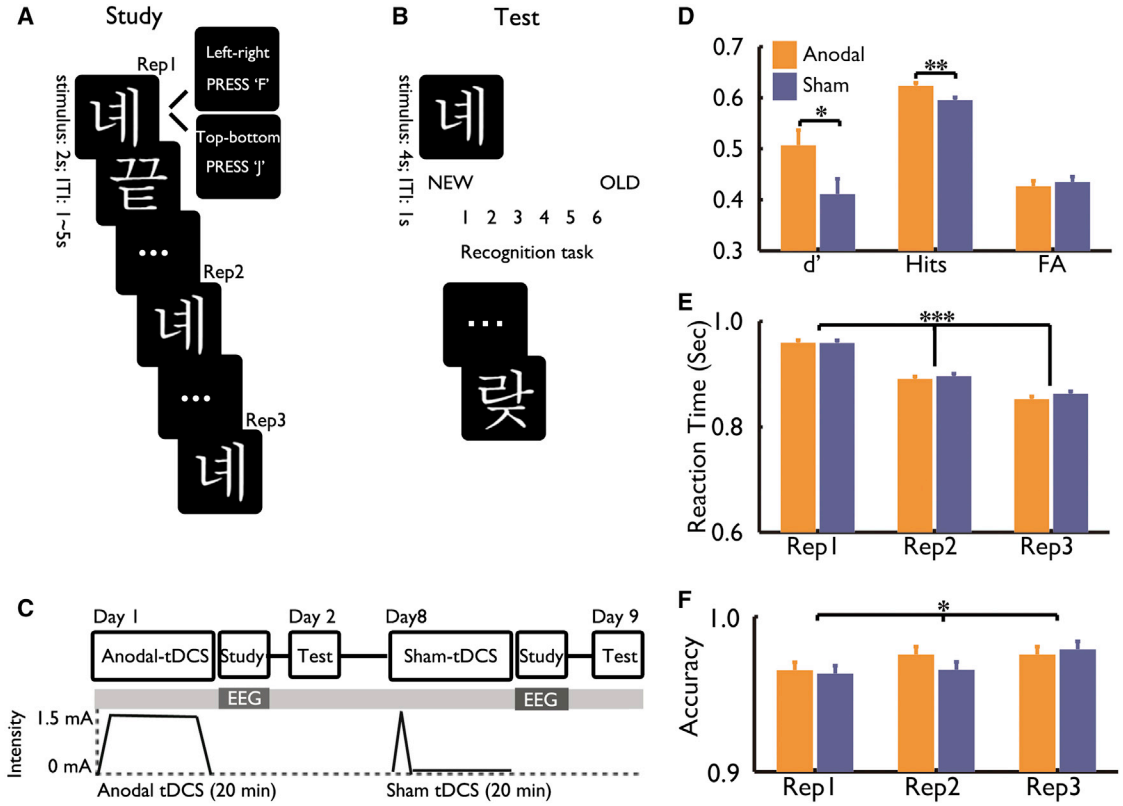

Figure 1. Experimental Paradigm and Behavioral Results

(A) The memory encoding task. Each of the 120 novel Hangul characters was presented three times with an IRI of 4–7 trials. Participants were asked to memorize each character and perform a visual structure (left-right or top- bottom) judgment task.

(B) The recognition test. Participants were asked to decide whether they recognized each character on a six-point scale, with 1 indicating "definitely new" and 6 indicating "definitely old."

(C) The tDCS procedure. Participants completed the tasks under two conditions (anodal tDCS and sham), separated by 5–7 days.

(D) The effect of LPFC anodal tDCS on subsequent memory performance.

(E and F) Accuracy (E) and reaction time (F) during memory encoding as a function of stimulation condition and repetition.

Error bars represent within-subject SE. **$p < 0.01$; *$p < 0.05$.

one in the right frontal region (region 2, 500–656 ms: $t(19) = 3.34$, $p = 0.003$; corrected $p = 0.036$), and the other in the left posterior region (region 5, 547–684 ms: $t(19) = 3.72$, $p = 0.002$; corrected $p = 0.056$), survived cluster-based multiple comparison correction (see Supplemental Experimental Procedures) (Figures 2C–2F), whereas the other two clusters did not (all $p > 0.195$).

This STPS's item specificity was supported by a significant interaction between subsequent memory and item specificity in the right frontal region (547–668 ms: $F(1,19) = 10.468$, $p = 0.004$; corrected $p = 0.029$) (Figures 2C and 2D). Post hoc t tests showed significantly greater within-item than between-item STPS for remembered items ($t(1,19) = 2.08$, $p = 0.05$) but greater between-item STPS than within-item STPS for forgotten items ($t(1,19) = 2.16$, $p = 0.04$), suggesting that only subsequently remembered items showed item-specific STPS during repeated learning.

Self-STPS Did Not Reflect Contextual Drift

The computational models of memory often assume a slow drift of internal context, which can explain many observations in memory, such as the spacing effect [21] and the temporal clustering effect [4, 22]. We found that the IRI during learning was comparable for subsequently remembered and forgotten items under both the anodal ($t(19) = -1.61$, $p = 0.12$) and sham ($t(19) = -0.88$, $p = 0.39$) conditions (Figure S2A), suggesting our results were not due to the spacing effect. Furthermore, we examined whether the recognized items were temporally clustered by comparing the average distance (in terms of the number of intervening items during the learning stage) between remembered items with the average distance between remembered and forgotten items [23]. This analysis revealed no evidence of temporal clustering for either anodal ($t(19) = -0.79$, $p = 0.44$) or sham ($t(19) = -0.71$, $p = 0.48$) condition (Figure S2B). It should be noted that since the current study used a recognition test and the sequence of old and new items were randomly mixed, it did not have enough statistical power to take the sequence of test order into consideration and to calculate the conditional response probability (CRP) as a function of lag (i.e., lag-CRP) [23].

We then examined whether the spatiotemporal responses also carried contextual information. If they did, the between-trial STPS would show a decline with increasing lag [24, 25]. We found no lag effect for between-item STPS in the two regions showing the subsequent memory effect (Figures S2C and S2D). Together, our analysis revealed no evidence that contextual drift contributed to STPS or subsequent memory (See Supplemental Discussion).

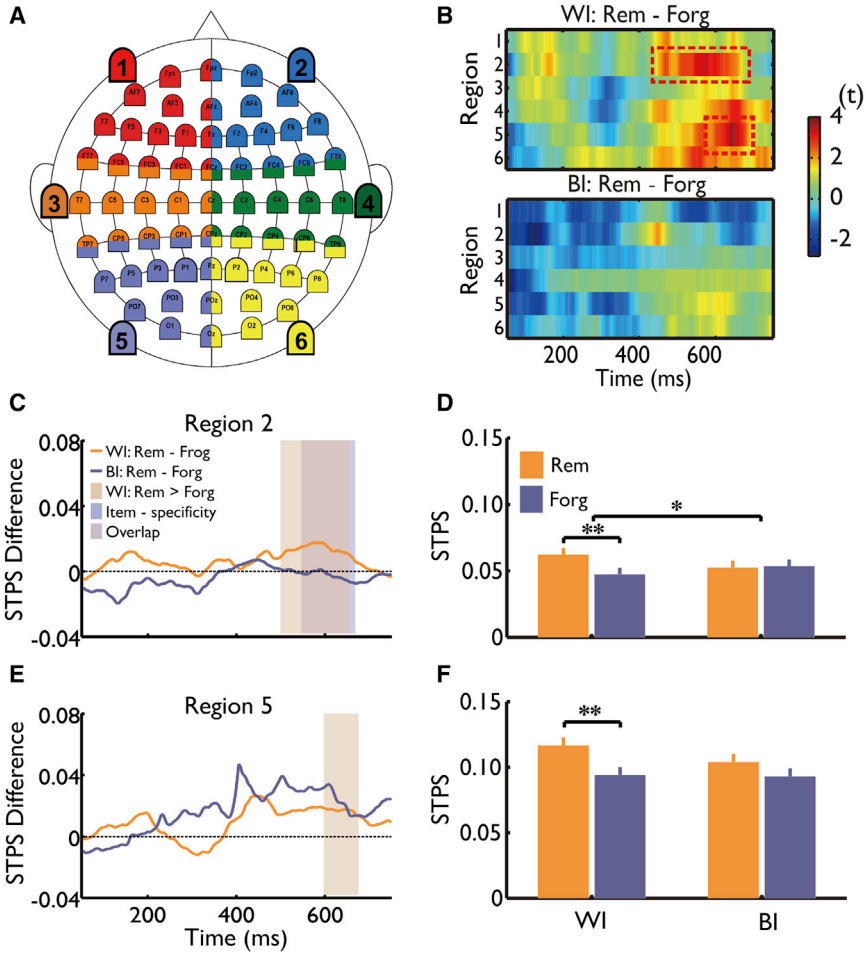

Figure 2. Self-STPS Predicted Subsequent Memory

(A) The 64 electrodes were grouped into six regions. To obtain more stable spatial patterns, we included the electrodes in the border of two regions in both regions.

(B) The statistics of the subsequent memory effect based on within-item (WI) STPS (top) and the between-item (BI) STPS (bottom). The x axis represents time, and the y axis represents the spatial locations.

(C) Plot of STPS differences, as a function of time and subsequent memory (remembered versus forgotten items) in Region 2. The shaded areas mark the temporal clusters showing significant effects after correction for multiple comparisons using cluster-based permutation.

(D) Bar graph of mean pattern similarity in the corresponding temporal cluster in Region 2, as a function of subsequent memory, separately for within-item and between-item STPS.

(E) Plot of STPS differences, as a function of time and subsequent memory (remembered versus forgotten items) in Region 5.

(F) Bar graph of mean pattern similarity in the corresponding temporal cluster in Region 5.

Error bars represent within-subject SE. **p < 0.01; *p < 0.05.

Controlling Signal Amplitude and Feature-Level and Trial-Level Variability

The above analyses suggested that subsequently remembered items showed greater item-specific STPS. Meanwhile, we also found a significant univariate effect in the event-related potential (ERP) amplitude (Supplemental Results). Although the Pearson correlation coefficients we used to calculate STPS were insensitive to the absolute amplitude and variance of the EEG response, existing simulation work suggests that feature-level (within-trial) variability, trial-level (cross-trial) variability [26], and mean signal amplitude [14] could all affect the pattern similarity estimation. Several control analyses were thus conducted, and the results confirmed that our conclusions were not affected by these factors (Supplemental Results and Figure S3).

Anodal tDCS Enhanced Item-Specific STPS

To test our hypothesis that LPFC tDCS could enhance item-specific STPS, we compared the self-STPS between anodal and sham stimulation for each of the six regions (Figure 3A). This analysis revealed that the right frontal region showed greater self-STPS under the anodal than under the sham stimulation condition in the 414–750 ms time window ($F(1,19) = 11.37$, $p = 0.003$; corrected $p = 0.015$) (Figure 3C). It is worth noting that this spatiotemporal cluster completely covered the cluster that showed the subsequent memory effect (500–656 ms). Furthermore, there was a significant interaction between tDCS condition and item specificity in the 480–656-ms time window ($F(1,19) = 16.24$, $p < 0.001$; corrected $p = 0.024$), suggesting that anodal tDCS significantly enhanced the self-STPS ($F(1,19) = 11.37$, $p < 0.001$), but not the between-item STPS ($F(1,19) = 2.02$, $p = 0.17$) (Figure 3D). A 480–601-ms temporal window in the right posterior region also showed a tDCS effect ($F(1,19) = 6.07$, $p = 0.023$), but this effect was not significant after correction ($p = 0.21$).

TDCS also enhanced univariate ERP amplitude (Supplemental Results) but did not affect the feature-level or trial-level variability in the regions showing significant tDCS effects on self-STPS (Figure S3). Simulation results confirmed that the tDCS effects were not due to differences in feature-level or trial-level variability (Figure S3). Linear mixed-effect model revealed that after controlling for the ERP amplitude, the tDCS effect on self-STPS in the right frontal region remained significant ($p = 0.001$).

Subsequent Memory Was Associated with Greater Global STPS

Existing computational models and fMRI studies suggest that self-similarity and global similarity might reflect different cognitive and neural processes related to subsequent memory [14, 15]. The global similarity reflects how similar the mental representation of one item is to those of other items in the memory space. To calculate the neural global STPS, we first averaged the EEG responses for each item across three repetitions. Global STPS was obtained by averaging the z-transformed similarity index (from Pearson correlation coefficients) with all other studied items [14]. Two posterior regions showed higher global STPS for subsequently remembered items than forgotten items (Figure 4A). The right occipital region survived the multiple comparison correction (422–582 ms, $t(19) = 2.902$,

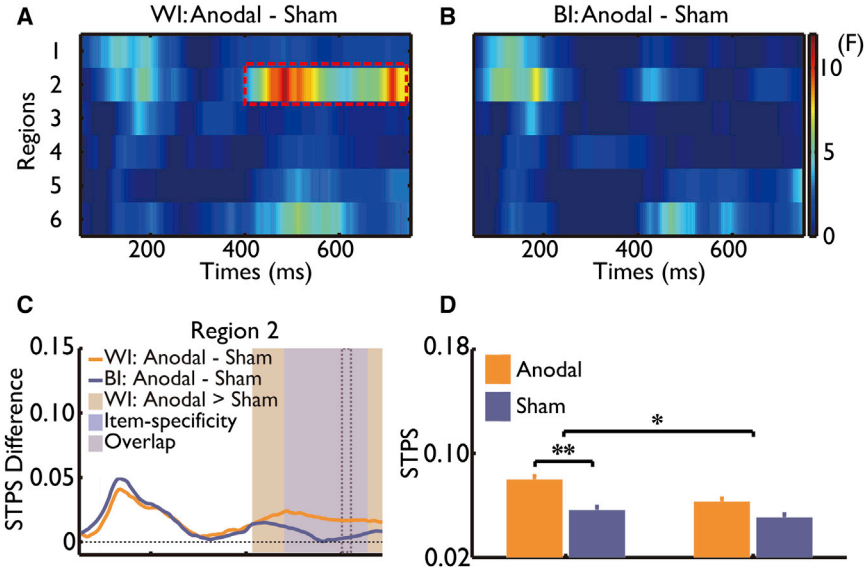

Figure 3. TDCS Effect on Self-STPS

(A) The statistics of the tDCS effect on within-item (WI) STPS.

(B) The statistics of the tDCS effect on between-item (BI) STPS.

(C) STPS differences as a function of time and stimulation condition (anodal versus sham stimulation), in Region 2.

(D) Mean STPS in the corresponding temporal clusters as a function of stimulation condition, separately for within-item and between-item STPS. Error bars represent within-subject SE. **p < 0.01; *p < 0.05. See Figure 2 for spatial location of the right frontal region.

p = 0.009; corrected p = 0.027) (Figures 4C and 4D), whereas the left occipital region did not (504–586 ms, t(19) = 3.367, p = 0.003; corrected p = 0.097). Linear mixed-effect model revealed that after controlling for the EEG amplitude, the effect remained marginally significant (p = 0.06) in the right occipital region.

As both self-STPS and global STPS contributed to subsequent memory, we also examined their unique contributions using the linear mixed-effect model. Results showed that self-STPS in the right frontal region (p = 0.015) and global STPS in the right occipital region (p = 0.078), which showed a robust subsequent memory effect after controlling for the EEG amplitude, remained significant after controlling for each other, suggesting they had independent effects on subsequent memory.

Anodal stimulation only had a marginally significant effect on global STPS, which was found in the right posterior region in the time window of 433–543 ms (F(1,19) = 7.145, p = 0.015; corrected p = 0.079) (Figures 4B and 4D). However, after controlling for the EEG amplitude, this effect was no longer significant (p = 0.17). Together, our results showed that self-STPS played a unique role in successful memory encoding and that tDCS over the left LPFC mainly enhanced self-STPS.

Control Experiment: The tDCS Effect Was Specific to LPFC

We did a control experiment to examine whether the tDCS effect was region specific. Since the encoding task required detailed visual analysis, we stimulated the posterior visual cortex to examine whether it could also enhance memory performance and pattern similarity. Seventeen additional subjects were recruited to perform the same experimental task, once under anodal stimulation and once under sham stimulation. We found that anodal tDCS, as compared to sham, significantly improved the accuracy (F(1,16) = 4.77, p = 0.04) during visual structure judgment (Figure S4A). Nevertheless, it did not change the reaction time (F(1,16) = 0.37, p = 0.55) (Figure S4B) or the memory performance as measured by the number of correct hits (t(16) = 1.01, p = 0.33) or d′ (t(16) = 0.41, p = 0.69)(Figure S4C).

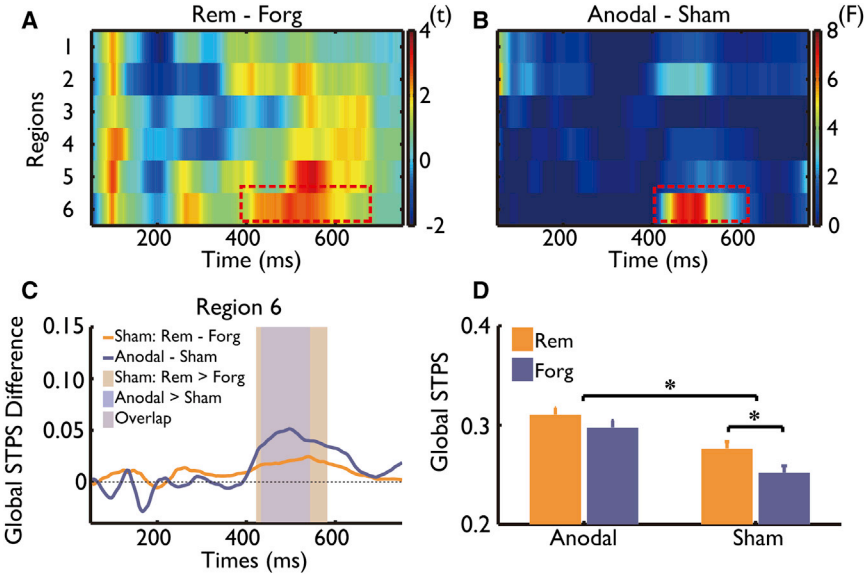

Figure 4. Global STPS and Subsequent Memory

(A) The statistics of the subsequent memory effect on global STPS.

(B) The statistics of the tDCS effect on global STPS.

(C) Global STPS differences as a function of time, subsequent memory, and stimulation condition in Region 6.

(D) Mean global STPS in the corresponding temporal clusters as a function of subsequent memory and stimulation condition. Error bars represent within-subject SE. **p < 0.01; *p < 0.05. See Figure 2 for spatial location of the right occipital region.

Consistently with our main experiment, EEG data indicated that two temporal clusters in the right frontal electrodes, one between 238 and 496 ms ($F(1,16) = 13.83$, $p = 0.004$; corrected $p = 0.04$) and the other between 527 and 746 ms ($F(1,16) = 8.66$, $p = 0.01$; corrected $p = 0.05$), showed greater STPS for subsequently remembered than forgotten items (Figures S4D–S4F). Notably, the temporal window of the second cluster showed much overlap with the cluster found in the main experiment. Again, STPS in the second cluster only reflected item-specific encoding as indicated by the significant subsequent memory by item specificity interaction ($F(1,16) = 5.46$, $p = 0.03$) (Figure S4F). Further analysis suggested that only remembered items showed greater within-item than between-item similarity ($F(1,16) = 11.45$, $p = 0.004$), whereas forgotten items did not ($F(1,16) = 0.08$, $p = 0.78$). Nevertheless, there was no significant main effect of tDCS ($F(1,16) = 1.23$, $p = 0.28$) or tDCS by subsequent memory interaction ($F(1,16) = 2.75$, $p = 0.12$) in this time window. If anything, we found that stimulation over the visual cortex slightly reduced STPS in the early time window ($F(1,16) = 5.96$, $p = 0.03$; corrected $p = 0.11$) (Figures S4G–S4I).

Discussion

Combining EEG with noninvasive brain stimulations via tDCS, the present study examined (1) the STPS's contributions to subsequent memory and (2) the LPFC's role in enhancing STPS and memory. Using representational similarity analysis on features from distributed electrodes and extended time windows, the current study replicated and extended the previous observation [27, 28] that the amplitude of neurophysiologic responses reflects item-specific encoding. Importantly, the STPS that contributed to successful memory encoding occurred at approximately 500 ms post-stimulus, most reliably in the right frontal scalp. This component was unlikely to be related to semantic processing [29], as the novel Korean characters contained no explicit semantics to the participants, and the latency was obviously later than the typical N400 component that peaks at around 350 ms. Instead, it has been consistently linked to memory retrieval in the literature [30]. Moreover, it could index memory reinstatement as this response differed according to the prior encoding history of the same stimuli [31–33].

The above finding suggests that one important source of the item-level STPS is the reactivation or reinstatement of existing memory trace, i.e., study-phase retrieval. Behavioral and computational studies have consistently suggested that during repeated studies, subsequent study episode serves as a retrieval cue to reactivate and strengthen the memory representation of the information stored during earlier study episodes [34, 35]. Imaging studies suggest that this study-phase retrieval is accompanied by the reactivation of early neural activation pattern [10, 11] that is similar to pattern reinstatement during recall [36, 37] or recognition [38].

The tDCS results showed a causal relationship between left LPFC activity and STPS. The left LPFC supports goal-directed top-down attentional control [39], and left LPFC stimulation can enhance selective attention [40] and reduce the vigilance decrement over time [41]. This improved attentional control can enhance task-relevant feature representations [42], leading to greater pattern similarity across repetitions [43]. In addition, due to the dense anatomical connectivity between the prefrontal cortex (PFC) and medial temporal lobe (MTL) [44], anodal tDCS can enhance their functional connectivity [45], resulting in stronger pattern reinstatement and thus greater pattern similarity [7, 9].

Although fMRI studies have often reported reinstatement in the posterior regions associated with perception, the current study, together with several previous ERP studies have consistently found reinstatement over the right anterior scalp [31–33]. Interestingly, we found that tDCS over the left LPFC enhanced the STPS in the right frontal electrodes. This functional asymmetry appears to be consistent with the hemispheric encoding/retrieval asymmetry (HERA) model [17], which posits that the left PFC regions are critically engaged in memory encoding, whereas the right PFC regions are involved in memory retrieval. Nevertheless, due to the poor spatial resolution and the methodological challenges in accurate source localization, the source of the EEG effect requires further examination (Supplemental Discussion).

Taken together, our results suggest that greater STPS during repeated study underlies successful memory encoding, probably by creating unique yet consistent inputs to the hippocampus, which facilitates pattern separation and avoids interference in later retrieval [46]. This STPS is partially contributed by study-phase retrieval in the late time window and can be enhanced by increasing the prefrontal cortex function via tDCS. These results help to deepen our understanding of the role of neural activation pattern similarity in memory formation. Future studies should examine whether and how other types of information, including context, can affect pattern similarity and memory (Supplemental Discussion).

Supplemental Information

Supplemental Information includes Supplemental Results, Supplemental Discussion, Supplemental Experimental Procedures, four figures, and one table and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.01.055.

Author Contributions

Y.L. and G.X. designed the experiment. Y.L. performed the experiment. Y.L., C.W., and G.X. analyzed the data. Y.L., C.C., and G.X. wrote the manuscript.

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