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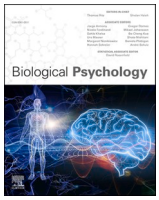

Peripheral nerve stimulation using tDCS can enhance reconsolidation but cannot mitigate retrieval-induced forgetting

Elva Arulchelvan [a,b], Caledonia Steltzner [b], Sven Vanneste [a,b,c,*]

[a] Lab for Clinical and Integrative Neuroscience, Trinity Institute for Neuroscience, School of Psychology, Trinity College Dublin, Ireland
[b] School of Psychology, Trinity College Dublin, Dublin, Ireland
[c] Global Brain Health Institute of Neuroscience, Trinity College Dublin, Dublin, Ireland

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ABSTRACT

Introduction: Memory reconsolidation refers to the process by which reactivated memories are rendered labile - and can be further strengthened or become sensitive to disruption. This study investigated whether non-invasive transcutaneous electrical stimulation of the greater occipital nerve (NITESGON) using direct current stimulation (tDCS) can modulate reconsolidation processes.

Methods: In a randomised, double-blind, placebo-controlled experiment, 38 healthy participants completed a Swahili-English paired-association task across three sessions over two consecutive days. Active or sham NITESGON was applied during reconsolidation, to test its effects on retrieval practice and retrieval-induced forgetting.

Results: Active NITESGON significantly enhanced memory reconsolidation, as evidenced by superior retrieval of previously consolidated pairs (i.e. *no-change* pairs) compared to sham stimulation. However, critically, we demonstrate that NITESGON did not mitigate retrieval-induced forgetting: both groups exhibited greater forgetting of competing associations (*competing* pairs) than non-competing ones (*original* pairs). This study also highlights how active NITESGON (compared to sham) significantly enhanced consolidation, but not acquisition or forgetting processes.

Conclusion: These findings demonstrate that peripheral nerve stimulation via tDCS can strengthen reconsolidation through retrieval practice, but does not alter retrieval-induced forgetting. This work elucidates the stage-specific influence of peripheral nerve stimulation on memory processes and highlights its potential translational value for conditions involving memory dysfunction.

1. Introduction

Once information is encoded, for it to be stored as a more stable, longer-lasting memory, it undergoes a process of consolidation (Squire et al., 2015). However, the maintenance of memories is a dynamic and active process (Nader, 2015). Accordingly, reactivation of a consolidated memory can trigger the process of reconsolidation. Thus, while acquisition, consolidation, retrieval (and recently forgetting) are acknowledged as stages in the memory process, over the last few decades, accumulating research has identified another critical stage: reconsolidation (Alberini & LeDoux, 2013; de Oliveira Alvares & Do-Monte, 2021; Nader, 2015). Reconsolidation refers to the phenomenon whereby consolidated memories can enter a labile state when reactivated, during which time they can be further strengthened or are sensitive to disruption (Alberini & LeDoux, 2013; Lee et al., 2017; Sandrini et al., 2015; Sinclair & Barense, 2019). In particular, it is increasingly accepted how the act of retrieval itself can initiate this process of reconsolidation (Alberini & LeDoux, 2013; Lee et al., 2017; Sandrini et al., 2015; Tronson & Taylor, 2007; Vaverková et al., 2020).

Retrieval refers to accessing information that is stored in our long-term memory, often through the use of cues (Roediger & Butler, 2011). Using transcranial direct current stimulation (tDCS) montages that target peripheral nerves, only one study to date previously examined peripheral nerve stimulation's impact on retrieval. In that study however, Non-invasive Transcutaneous Electrical Stimulation of the Greater Occipital Nerve (NITESGON) was applied at the time of retrieval

* Correspondence to: Lab for Clinical & Integrative Neuroscience, School of Psychology, Global Brain Health Institute, Institute of Neuroscience, Trinity College Dublin, College Green 2, Dublin, Ireland.
E-mail address: sven.vanneste@tcd.ie (S. Vanneste).

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and found no significant effect, moreover it did not look specifically at reconsolidation (Vanneste et al., 2020). One means through which reconsolidation can be assessed is through the use of retrieval practice. Retrieval practice involves repeatedly retrieving previously learnt information with the intention of improving our memory for them. While the benefits of retrieval practice are well-established, no studies to-date have investigated whether peripheral nerve stimulation using tDCS can enhance reconsolidation via retrieval practice.

From a neurobiological perspective, NITESGON represents a particularly appropriate intervention for modulating reconsolidation processes. Although non-invasive neurostimulation techniques such as tDCS were initially conceptualised as exerting their effects through direct transcranial modulation of cortical activity, accumulating evidence indicates that stimulation applied to the head or neck can act through indirect transcutaneous peripheral nerve pathways (Asamoah et al., 2019; van Boekholdt et al., 2021; Vöröslakos et al., 2018; Woods et al., 2016). For example, when stimulation is applied over the C2 nerve dermatome, a substantial proportion of current is argued to pass through the greater occipital nerve. These greater occipital nerve afferents converge onto neurons in the spinal trigeminal nucleus caudalis within the trigeminocervical complex, which synapse on to brainstem nuclei such as the nucleus tractus solitarius, subsequently activating locus coeruleus – noradrenaline projections across cortical and subcortical regions (Goadsby et al., 2008; Luckey et al., 2023).

Noradrenergic and dopaminergic signalling from the locus coeruleus and ventral tegmental area play central roles in memory reconsolidation, influencing hippocampal synaptic plasticity and the re- or destabilisation of reactivated memory traces (Hansen, 2017; Haubrich et al., 2020; Pigeon et al., 2022; Sara, 2009). Consistent with this framework, recent work from our laboratory has demonstrated that NITESGON supports memory consolidation and retention via locus coeruleus–mediated noradrenergic modulation of hippocampal activity (Luckey et al., 2023; Vanneste et al., 2020). Accordingly, NITESGON's neuromodulatory mechanisms position it as an intuitive non-invasive stimulation technique to modulate memory reactivation processes. Thus, this experiment aimed to novelly test whether tDCS of the greater occipital nerve (i.e. NITESGON) could enhance memory reconsolidation. Specifically, it sought to investigate whether NITESGON could enhance memory of previously consolidated information using a paradigm involving retrieval practice.

As mentioned above, reconsolidation can both strengthen memories, or render them more susceptible to interference (Alberini & LeDoux, 2013; Lee et al., 2017; Sandrini et al., 2015). Related to this, established research has highlighted how the act of retrieval can both support the maintenance of certain memories or induce forgetting of others, with this phenomenon aptly termed *retrieval-induced forgetting* (Anderson et al., 1994; Hulbert & Anderson, 2020; Miller, 2021; Murayama et al., 2014). Retrieval-induced forgetting is often investigated through the use of cue-target paradigms where retrieval of some items from memory (e.g. A-B cue-target pairs) will enhance their retention, while also inhibiting the retention of other related items (especially those associated with the same cue, e.g. A-C pairs). However, critically, prior research has not only neglected to specifically investigate whether peripheral nerve stimulation can enhance reconsolidation via retrieval practice, but likewise it has failed to examine whether it can prevent retrieval-induced forgetting.

Across drosophila and rodents, the dopaminergic system has been implicated in regulating the persistence or forgetting of memories (Berry et al., 2024; Castillo Díaz et al., 2021). In rodents, it has been shown that blocking specific dopamine receptors in the medial prefrontal cortex impaired retrieval-induced forgetting (Gallo et al., 2022). Supporting this, in humans one study demonstrated how dopamine availability impacted retrieval-induced forgetting. Specifically, genetic markers associated with greater levels of prefrontal cortical dopamine predicted increased rates of retrieval-induced forgetting (Wimber et al., 2011).

Thus, these studies suggest that dopamine facilitates adaptive forgetting of competing memories in prefrontal-mediated memory control. Given NITESGON has been shown to modulate dopaminergic as well as noradrenergic activity (Luckey et al., 2023), it is conceivable that it may also alter forgetting dynamics during retrieval. However, prior behavioural work by our lab suggests a more selective pattern: previously we observed that NITESGON enhanced consolidation but did not modulate forgetting rates in older adults (Luckey et al., 2020). This raises an important open question: does peripheral nerve stimulation strengthen memories during reconsolidation without altering inhibitory forgetting processes, or can it influence both?

The present study aimed to address this gap by testing whether NITESGON modulates memory during reconsolidation triggered by retrieval practice. Specifically, we examined whether stimulation enhances retention of previously consolidated information following reactivation, and whether it alters retrieval-induced forgetting of competing memories. Based on prior findings (Luckey et al., 2023; Luckey et al., 2020), we hypothesized that NITESGON would enhance reconsolidation via retrieval practice but would not significantly modulate retrieval-induced forgetting.

Importantly, retrieval practice and retrieval-induced forgetting have clinical implications in conditions such as schizophrenia or prodromal stages of Alzheimer's disease (Ebert & Anderson, 2009; Hanseeuw et al., 2012; Jantzi et al., 2019). Moreover, whether the declarative components of memories can be modulated through reconsolidation-based neurostimulation approaches is likewise relevant for conditions such as post-traumatic stress disorder (PTSD) or addiction-related disorders (Alberini & LeDoux, 2013; Lee et al., 2017; Sandrini et al., 2015). Thus, investigating these questions will not only help with our mechanistic understanding of peripheral nerve stimulation's impact on memory processes, but also may outline future therapeutic avenues worth investigating.

2. Methods

2.1. Participants

Forty participants were recruited to participate in this study. Participants were screened to ensure normal or corrected-to-normal vision, no transcutaneous electrical stimulation (tES) contraindications including no neurological or psychiatric diagnoses, no taking of neuropsychiatric medications or prescription stimulants, and no chronic use of illicit drugs. Participants were native English speakers, with no prior familiarity or exposure to Arabic language or Swahili (due to task stimuli).

Validated measures including the Beck Depression Inventory – II (BDI-II), Beck Anxiety Inventory (BAI) and Mini Mental State Exam (MMSE) were administered to each participant at the start of visit one to measure cognition, anxiety or depression levels. If standard cut-off values were exceeded on these measures, participants were excluded from participating. For example, based on standard procedures, participants were excluded from participating if they scored > 20 on the BDI-II indicating moderate/ severe depression, > 16 on the BAI indicating moderate/ severe anxiety, or > 24 on the MMSE indicating probable mild cognitive impairment (Bardhoshi et al., 2016; Mitchell, 2017; Whisman & Richardson, 2015).

Alongside these measures, demographic variables were also collected to ensure that any between-group behavioural differences were specifically due to the effects of the stimulation. In addition, given that sleep can impact consolidation, participants were asked to indicate the quality (out of 10) and length (hours) of their sleep the night before each session. This enabled us to ensure that if there were any differences between groups after receiving stimulation, that this was not due to a sleep-specific benefit.

One participant was excluded from participating for exceeding the BAI cut-off score. One other participants' data was excluded due to software malfunction resulting in incomplete data. This resulted in 38

participants' data being analysed (11 males and 27 females: mean age 20.42 years, SD = 2.21 years)(See Table 1 for demographic information and control measure results).

An a priori power analysis was performed in G*Power (Faul et al., 2009) to estimate the sample size necessary to detect a significant difference in memory between active and sham conditions, assuming a medium effect size derived from previous literature on peripheral nerve stimulation (Luckey et al., 2023; Luckey et al., 2020; Vanneste et al., 2020). Results indicated that 38 participants would yield 93% power to detect effects at $\alpha = .05$. Allowing for an expected 5% attrition rate, the planned sample size was set at 40 participants.

2.2. Materials

2.2.1. NITESGON

Non-invasive transcutaneous electrical stimulation of the greater occipital nerve (NITESGON) using direct current was delivered using a specially developed, battery-powered, constant-current stimulator with a maximum output of 10 mA (http://www.neuroconn.de) via a pair of saline-soaked surface sponges (35 cm2) on the scalp. Stimulation parameters (electrode location, stimulation intensity, ramp up/ down details and sham conditions) were in line with prior research (Luckey et al., 2023; Luckey et al., 2020; Vanneste et al., 2020). Electrodes were placed on the left and right C2 nerve dermatome, and impedance under each electrode was maintained under 10 kΩ.

In Session 2, participants were randomly assigned to one of two groups: active NITESGON or sham NITESGON. For active NITESGON, stimulation ramped up for 30 s, a constant current of 1.5 mA intensity was applied during each of the 3 study phases of the task (i.e. 375 s × 3 blocks), and stimulation ramped down for 5 s. For sham NITESGON, placement of the electrodes was identical to active NITESGON. At the start of each study phase, stimulation ramped up for 30 s, was applied for 15 s only (to mimic the sensation), and ramped down for 5 s. No stimulation was applied during rest or testing phases for either group, and no stimulation was applied during Session 1 or Day 2 for either group. See Fig. 1 for the stimulus protocol.

2.2.2. Paired association task

Participants completed a computerized Swahili-English word association task, using word-pairs from Nelson and Dunlosky (1994) study. The task was adapted from a well-established paradigm by Karpicke and Roediger (2008), and amended following standard interference-based and retrieval-induced forgetting paradigms (Anderson & Neely, 1996). The task was designed using PsychoPy software. In Session 1, participants learned 60 randomly presented Swahili-English cue-target pairs. These pairs were made up of 3 lists of 20 cue-target pairs (termed *original* pairs, *competing* pairs and *no-change* pairs). In Session 2 on Day 1, 60 Swahili-English cue-target pairs were also presented. However, this list varied slightly. Twenty of these pairs had the same Swahili cue but a different English target to the *original* pairs. These were termed *competing* pairs). For example, lozi-almond (*original* pair shown in Session 1) versus lozi-oval (*competing* pair shown in Session 2). Another 20 pairs were the exact same cue-target pairs as Session 1 (i.e. the *no-change* pairs), and the remaining 20 were novel cue-target pairs (termed *stim-only* pairs because they were only presented for learning during Session 2 where stimulation was applied) (See Fig. 2 for task design and examples of the stimuli sets). The presentation of these word pairs at each session was randomized, meaning participants were unaware that the pairs they were learning were made up of 3 separate lists.

The task in both Session 1 and Session 2 followed the same format but with slightly different instructions. It involved 3 blocks, each with a study and test phase. In the study phase, each Swahili-English word pair (e.g. Bustani – Garden) were shown on screen for 5 s at a time, with the Swahili word on top, and English translation underneath, with a 1 s break in between each pair (i.e. (5 s × 60 pairs) + (1 s × 60 pairs) = 360 s). Words were presented in black on a white background. A 30 s rest separated the study phase from the test phase. The test phase followed standard retrieval practice format. Here, each Swahili cue word was randomly presented on screen for 8 s (with a 1 s break in between each), and the participant was tasked with typing the English translation. If no response was given, the computer program automatically moved onto the next Swahili cue. This cycle was repeated twice more. Any correctly recalled pairs from the 1st and 2nd testing phases were dropped from being tested in subsequent test phases (but were still presented in all 3 study phases). This meant that the study phase was always 360 s per block, with 3 blocks in total. However, the length of the retrieval test phase varied for each participant depending on how many words they had correctly learned in the previous block. Word order was randomized in each phase and block. Cumulative rates of learning were calculated across the 3 test phases. In Session 1, participants were instructed to try to learn as many pairs as possible. In Session 2, the instructions varied slightly in that participants were informed that some of the pairs may be the same or different to those presented in the earlier session, but their task was still to try to learn as many pairs as possible.

When participants returned for the final visit the next day, they completed only 2 retrieval testing-phase blocks of the task. In the first block, they were asked to recall the English targets of the Swahili cues that were presented in Session 1 the previous day. Sixty cues were randomly presented in this block from the *original*, *no-change* and *baseline* pairs. In the second block, they were asked to recall the English targets of the Swahili cues that had been presented in Session 2 the previous day. In this block, 40 Swahili cues were randomly presented from the *competing* and *stim-only* pairs. When each Swahili cue was presented on screen, their task was to type the correct English translation. There were no review of word-pairs and no stimulation on this visit. The structure of this word-association paradigm is presented in Fig. 2 and Fig. 3.

As such, *original* and *baseline* pairs were used to test baseline learning in Session 1 for the two stimulation groups, with no differences between stimulation groups expected. Given prior research which demonstrated no effect of NITESGON on acquisition (Luckey et al., 2023; Luckey et al., 2020), it was also expected that there would be no differences between the stimulation groups in learning rates for *competing* and *stim-only* pairs in Session 2.

Table 1
Average control measures of the stimulation groups.

	Active	**Sham**		
N	18	20		
			χ^2	***p***
Sex	Male (N = 4) Female (N = 14)	Male (N = 7) Female (N = 13)	.75	*.386*
Gender	Man (N = 4) Woman (N = 14) Non-binary (N = 0)	Man (N = 5) Woman (N = 14) Non-binary (N = 1)	1.01	.604
Handedness	LH (N = 3) RH (N = 15)	LH (N = 4) RH (N = 16)	.07	.791
Sleep quality			8.92	.259
Sleep quality			12.58	*.083*
			F	***p***
Age	20.5 (2.73)	20.35 (1.69)	.04	*.838*
MMSE	29.22 (0.88)	29.15 (1.09)	.05	*.825*
BDI	4.72 (3.25)	4.5 (0.95)	.03	*.859*
BAI	4.17 (3.28)	4.35 (4.39)	.02	*.886*
Sleep length (hours: night prior to Day 1)	6.9 (0.71)	7.8 (1.5)	5.10	*
Sleep length (hours: night between Day 1 and 2)	7.64 (1.17)	7.07 (1.19)	2.24	*.143*

Abbreviations include: Left-handed (LH), Right-handed (RH), Mini Mental State Exam (MMSE), Beck Depression Inventory (BDI) and Beck Anxiety Inventory (BAI). * $p < .05$

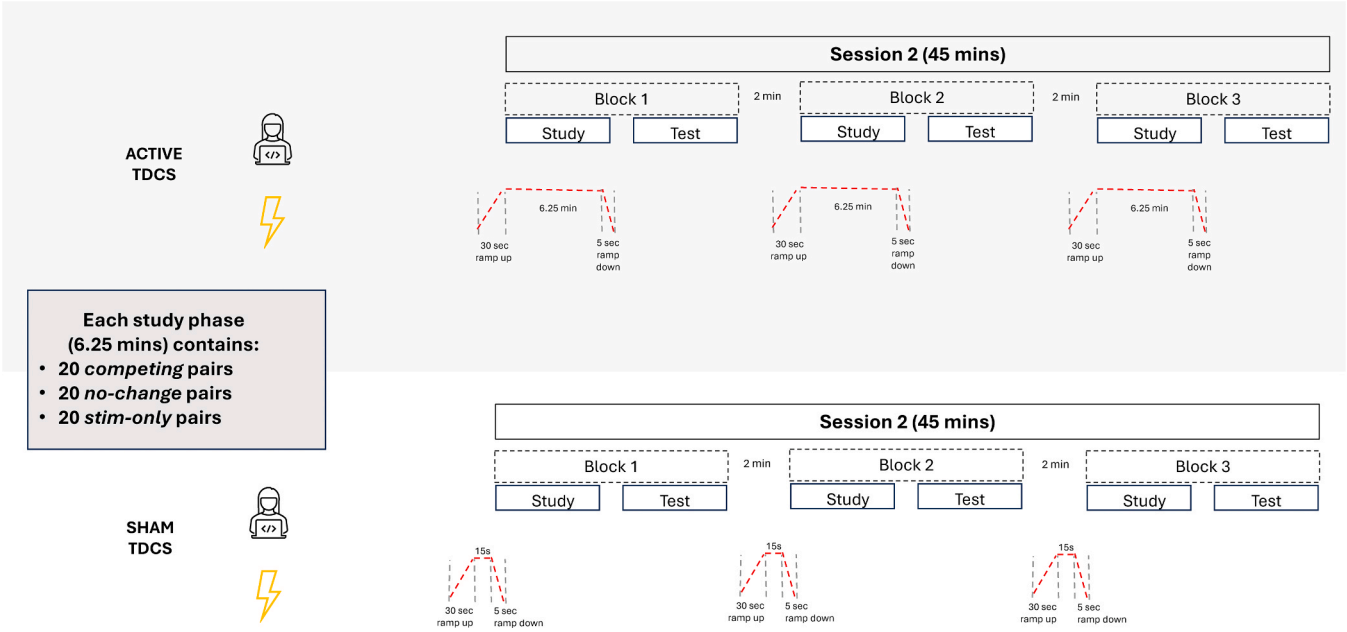

Fig. 1. Session 2 Stimulation Protocol. In Session 2, active stimulation was applied for each of the three study phases, while sham stimulation ramped up and down immediately prior to each study phase to mimic the sensation.

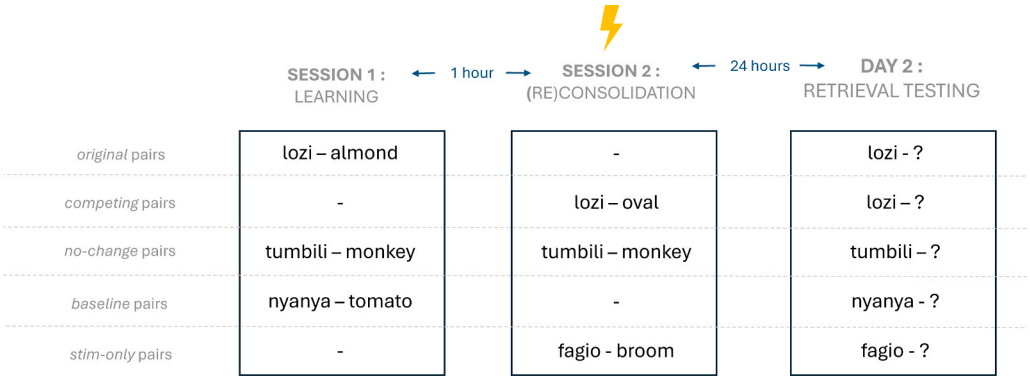

Fig. 2. Task Design and Stimuli Sets. In Session 1, *original*, (*no-change* and *baseline* pairs were randomly presented. In Session 2, *competing*, *no-change* and *stim-only* pairs were randomly presented. These sessions were separated by a 1-hour break. The following day, participants returned for a retrieval test of all of these pairs.

To compare consolidation rates, on Day 2 memory retrieval for the different pair lists was tested. It was expected that consolidation for the *baseline* and *original* pairs would not differ between groups. Whereas, given NITESGON's effects on consolidation (Luckey et al., 2023; Luckey et al., 2020), it was hypothesised that on Day 2, memory retrieval for the *competing* and *stim-only* pairs would be greater for the active group than the sham group.

The *no-change* pairs were presented during both Session 1 and Session 2. Critically, these pairs served to test whether NITESGON could enhance memory by boosting reconsolidation via retrieval practice. Reconsolidation can render a memory labile upon reactivation or retrieval. Both reconsolidation and retrieval can support the maintenance of certain memories or induce forgetting of others. Given that the *original* and *competing* pairs involved the use of the same Swahili cues but different English translations (i.e. lozi-almond versus lozi-oval), these pairs served to assess whether NITESGON could support the maintenance and reconsolidation of memories by minimising retrieval-induced forgetting. In other words, if retrieval for both *original* and *competing* pairs were greater for the active group than the sham group on Day 2, this would suggest enhanced reconsolidation due to NITESGON. Conversely, if from Day 1 to Day 2 more *competing* pairs were forgotten than the *original* pairs (with no differences between stimulation groups), this would indicate retrieval-induced forgetting was not mitigated by NITESGON.

2.2.3. tES Exit Questionnaire

To assess possible side effects of NITESGON, post-stimulation participants completed the tES Exit Questionnaire (Brunoni et al., 2011). It asked participants to rate (using a 4-point scale from 1 = absent to 4 = severe) the extent to which they might have felt symptoms (incl. headache, neck pain, scalp pain, tingling, itching, burning sensation, skin redness, sleepiness, trouble concentrating, or acute mood changes). If any were experienced, participants were asked to indicate (yes/no) whether they believed each symptom was related to the application of NITESGON. To determine if the stimulation was well-blinded, an item asked participants to guess, based on their experience, which stimulation they believed they had received (active or non-active).

2.3. Procedure

This study was designed as a double-blind, placebo-controlled, randomized parallel group study. It was granted ethical approval by the

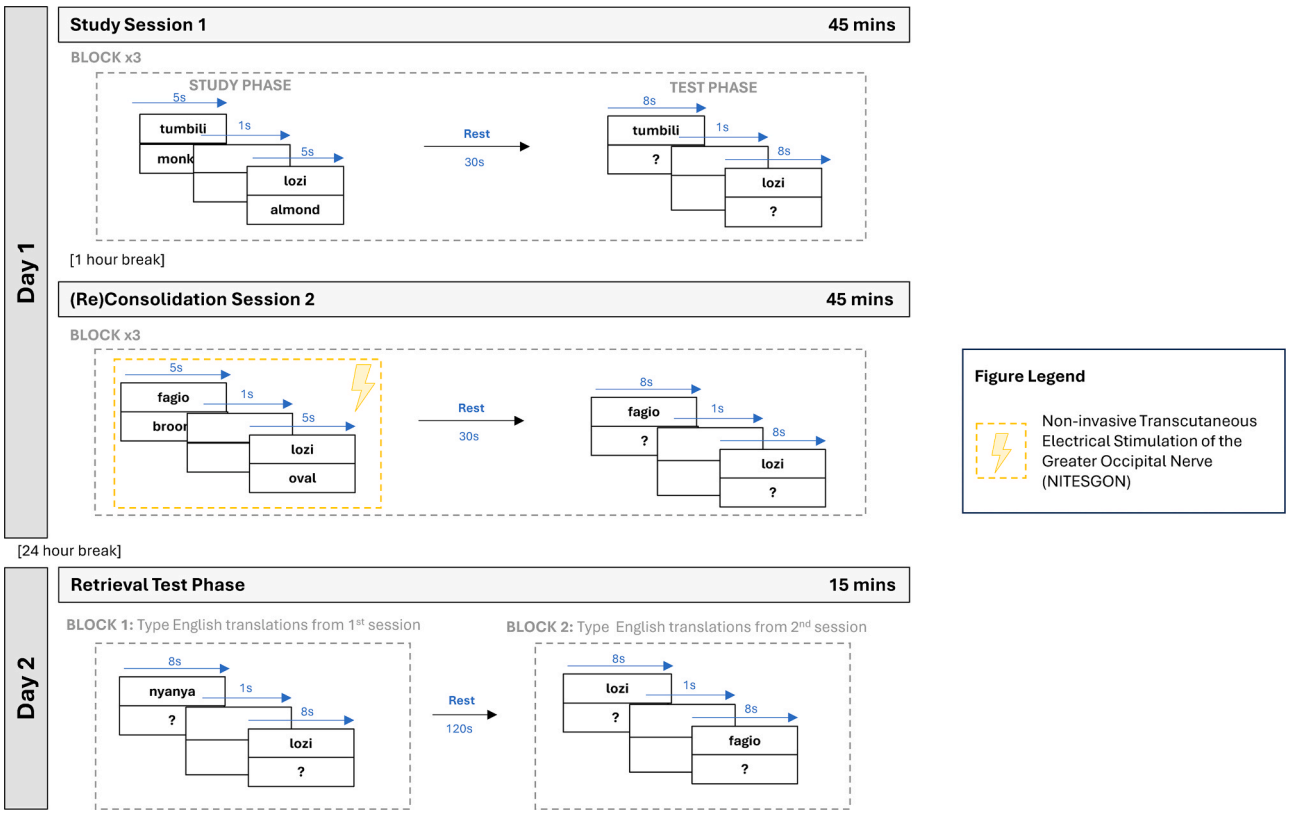

Fig. 3. Trial Design. In Session 1, there were 3 blocks each consisting of a study and test phase. In the study phase, Swahili-English word pairs were presented on screen for 5 s with a 1 s blank screen in between. A 30 s rest period followed, before the retrieval test phase began. In the test phase, the Swahili word was shown on screen for 8 s while the participants were tasked with typing the English translation, with a 1 s blank screen in between each stimuli. Session 2 followed the same format, except active or sham stimulation was applied at each of the study phases. 24 h later, participants returned for the retrieval test phase. There were 2 blocks, where participants were asked to type the English translations to the Swahili cues they learned the day prior, either in the first or second session, respectively.

Research Ethics Committee of the School of Psychology at Trinity College Dublin (Approval number: SPREC052022–08) and conducted in accordance with the ethical guidelines of the Helsinki declaration (1964).

Participation involved three visits to Trinity College Dublin. Session 1 and Session 2 were conducted on Day 1 (with a 1-hour break in between the two). 24 h later, participants returned for the Day 2 session, which took place at the same time as their Session 1 the day prior. In Session 1, participants completed control assessments incl. a sleep questionnaire, the Mini Mental State Exam (MMSE), Beck Anxiety Inventory (BAI), and Beck Depression Inventory (BDI-II), followed by a computer-based word-association task. In Session 2, participants returned and completed a related computer-based word-association task, whilst receiving active or sham NITESGON. A second researcher administered the stimulation, ensuring that the researcher who instructed the participant and conducted the analysis was blind to the stimulation protocol. At the end of this session, participants completed the stimulation exit questionnaire. Participants returned the following day to test memory performance. At the end of this session, they completed a final sleep-based questionnaire and were debriefed. Upon completion, participants could choose to be reimbursed monetarily for travel compensation, or to receive course credits where relevant.

2.4. Statistical analysis

All analyses were conducted using JASP (version 0.19.1.0).

2.4.1. Paired association task

On Day 1, cumulative learning rates (percentage of correctly learnt words from blocks one to three) were calculated for each of the *original, competing, no-change, baseline* and *stim-only* pair lists. On Day 2, the percentage of correctly recalled words from each list of pairs were calculated to examine memory recall. Forgetting rates i.e. percentage of pairs from each list that were forgotten were calculated by subtracting Day 1 scores from Day 2. To assess Session 1 learning rates, 3 one-way ANOVAs were conducted with the pair list of interest as the dependent variable and stimulation group (active/ sham) as the independent variable. To assess Session 2 learning rates, 3 one-way ANOVAs were likewise conducted with the pair list of interest as the dependent variable and stimulation group (active/ sham) as the independent variable.

To compare memory recall on Day 2 between the stimulation groups, 5 one-way ANOVAs were conducted with recall rate for pair list of interest as the dependent variable and stimulation group (active/ sham) as the independent variable.

To compare forgetting rates from Day 1 to Day 2 between the stimulation groups, 5 one-way ANOVAs were conducted with the forgetting rate for the pair list of interest as the dependent variable and stimulation group (active/ sham) as the independent variable.

To investigate whether NITESGON could mitigate retrieval-induced forgetting, a repeated measures ANOVA was conducted with stimulation group (active/sham) as the between-subjects variable and retrieval rates on Day 2 (for the *original* pairs and *competing* pairs) as the within-subject variables. If significance was obtained, a post-hoc analysis was applied to compare the different conditions using a Bonferroni correction. Additionally, a repeated measures ANOVA with stimulation group (active/ sham) as the between-subjects variable and forgetting rates of *original* and *competing* pairs as the within-subjects variables was conducted.

2.4.2. Control measures

One-way ANOVAs were conducted to examine whether there was a difference between the stimulation groups (active vs sham) for age (years), average sleep quality and length (hours) on the night prior to Day 1 and the night between Day 1 and Day 2 sessions, and MMSE, BDI, and BAI scores. Chi-square ($\chi 2$) tests were calculated to compare if there was a difference between the active and sham group for sex, gender and handedness.

2.4.3. tES exit questionnaire

To analyse whether participants were blinded to their stimulation group, Chi-square ($\chi 2$) tests compared the stimulation participants received (active vs sham) to what they thought they received (active vs non-active). A MANOVA was conducted to compare whether there was any difference between groups for experiencing common stimulation side-effects.

3. Results

3.1. Paired association task

The main aim of this research was to determine whether NITESGON delivered via tDCS influences memory performance by enhancing reconsolidation following retrieval practice and/or by modulating retrieval-induced forgetting, thereby clarifying which memory processes are behaviourally sensitive to stimulation. However firstly, baseline levels of learning were assessed, and tests were run to validate NITESGON's effects on consolidation (but not acquisition or forgetting).

3.1.1. Baseline learning and memory levels, and validating prior research

There were no significant differences between the groups in learning rates for any of the stimuli (i.e. *original* and *baseline* pairs) presented only during Session 1 (when no stimulation was applied). These results demonstrate equal baseline rates of learning for the two groups. The results of these statistical analyses are outlined in Table 2.

As expected, at Session 2 (when active/ sham stimulation was applied), there were also no significant differences between the groups in learning rates for *competing* and *stim-only* pair lists. See Table 2 for these results. Furthermore, as expected, on Day 2, there were significant differences between groups in memory retrieval only for the pair lists that had been presented during Session 2 the day prior (when active/ sham stimulation was applied), with the active group correctly remembering more of *competing* and *stim-only* pair lists than the sham group. See Table 2 for the full results of these statistical tests. These results are in line with prior research, and validate how NITESGON using tDCS does not enhance acquisition of newly learnt information, but rather boosts consolidation processes.

In addition, as expected, there were no significant differences between groups in the forgetting rates of each of the lists of word pairs. See Table 2 for these results. This further supports the argument that NITESGON enhances memory through upregulating consolidation, not by upregulating acquisition or downregulating forgetting processes.

3.1.2. Can NITESGON enhance reconsolidation?

The abovementioned results indicate that improved memory in response to NITESGON may stem from upregulated consolidation (and not downregulated forgetting). However, this study sought to novelly investigate whether NITESGON could enhance memory by boosting reconsolidation via retrieval practice. Critically and interestingly, in Session 2, there was a significant difference between groups in learning of the *no-change* pairs ($F(1, 36) = 4.15$, $p = .049$, $\omega^2 = .077$), with the active group ($M = 90.28$, $SD = 12.30$) remembering significantly more of the *no-change* pairs than the sham group ($M = 80.00$ $SD = 17.92$)(See Fig. 4b). This result of $\omega^2 = .077$ suggests that this was a moderate effect. This was the only list of pairs in Session 2 where there was a significant difference between groups (see Table 2). Given that the *no-change* pairs

Table 2
Summary of ANOVA Results.

	Session 1 (Learning)					Session 2 ((Re)Consolidation)					Day 2 (Retrieval)					Forgetting Rates				
	Active	Sham	F	*p*	ω^2	Active	Sham	F	*p*	ω^2	Active	Sham	F	*p*	ω^2	Active	Sham	F	*p*	ω^2
original pairs	68.06 (19.19)	59.25 (17.87)	2.16	*.15*	.030						55.28 (19.81)	46.25 (14.41)	2.62	*.11*	.041	-12.78 (9.24)	-13.00 (10.93)	.00	*.95*	.000
competing pairs						74.44 (18.93)	63.50 (24.98)	2.28	*.14*	.032	52.78 (20.09)	38.50 (21.91)	4.54	*.040*	.085	-21.68 (10.29)	-25.00 (13.38)	.73	*.40*	.000
no-change pairs	65.57 (21.34)	59.25 (19.15)	0.92	*.35*	.000	90.28 (12.30)	80.00 (17.92)	4.15	*.049*	.077	80.83 (15.65)	69.50 (17.54)	4.38	*.044*	.082	-9.44 (7.84)	-10.50 (8.72)	.15	*.70*	.000
baseline pairs	66.67 (19.93)	59.00 (25.27)	1.06	*.31*	.002						52.50 (19.19)	42.75 (20.87)	2.23	*.14*	.031	-14.17 (10.74)	-16.25 (8.72)	.44	*.51*	.000
stim-only pairs						77.50 (19.67)	63.25 (26.02)	3.57	*.07*	.063	64.17 (18.25)	49.25 (24.51)	4.44	*.042*	.083	-13.33 (9.70)	-14.00 (9.40)	.05	*.83*	.000

Notes. This table contains average percentage (and standard deviation) of learning, recall and forgetting rates for the active and sham groups at each of the testing points.

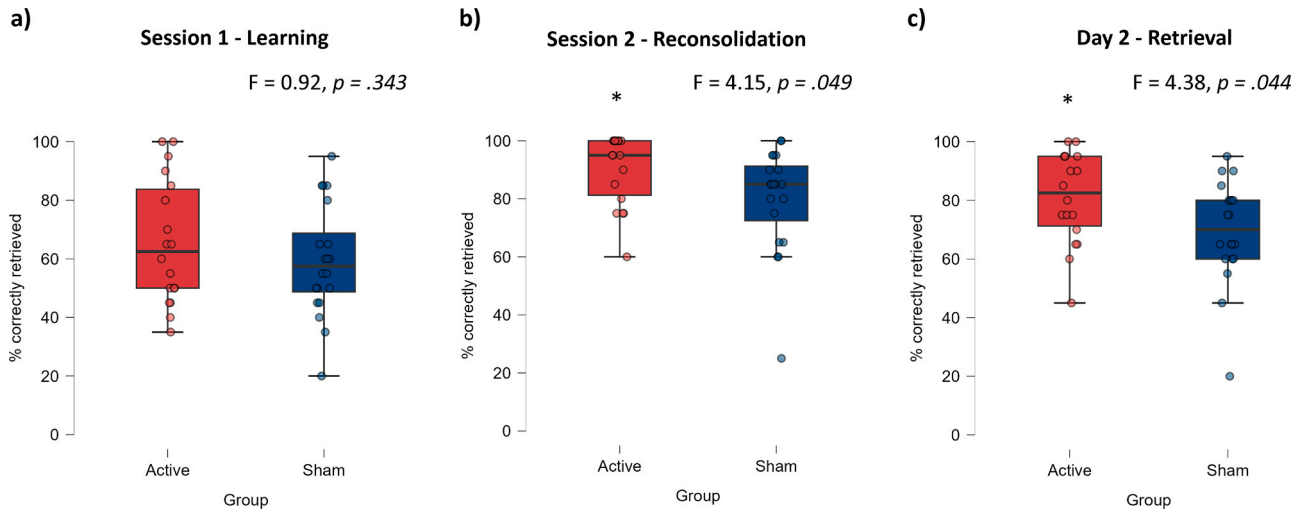

Fig. 4. Effect of Reconsolidation and Stimulation. a There were no significant differences between the active and sham groups in the retrieval of D-E pairs in Session 1. b However, when these pairs were presented again in Session 2 where active or sham stimulation was applied, there was a significant difference between the groups, with the active group retrieving more *no-change* pairs than the sham group. **c** Similarly, on Day 2, the active group retrieved significantly more *no-change*pairs than the sham group, demonstrating NITESGON's memory enhancement effect on retrieval practice.

had also been presented in Session 1 (where there were no significant differences between groups, see Fig. 4a), this suggests that for previously consolidated information, NITESGON can upregulate retrieval practice, further boosting reconsolidation of this information. This boost in reconsolidating the *no-change* pairs, subsequently led to significantly enhanced retrieval on Day 2, as outlined in Table 2 and Fig. 4c. See supplementary materials for additional analyses checking for outliers and verifying NITESGON's effect on reconsolidation.

3.1.3. Can NITESGON mitigate retrieval-induced forgetting during reconsolidation?

On Day 2, when comparing active and sham groups and looking at memory recall rates for the *original* and *competing* pairs, no significant effect of stimuli type was found ($F(1, 36) = 3.40$, $p = .073$, $\omega^2 = .013$) (See Fig. 5a). Although there was no significant effect for stimuli, this difference was most pronounced for *competing* stimuli, where the sham group recalled less on average. Interestingly however, there was a significant difference between the groups ($F(1, 36) = 4.48$, $p = .041$, $\omega^2 = .045$), with the active group remembering more pairs (*Original* Pairs: M = 55.28, SD = 19.81; *Competing* Pairs: 52.78, SD = 20.09) than the sham group (*Original* Pairs: M = 46.25, SD = 14.41; *Competing* Pairs: 38.50, SD = 21.10) on Day 2.

This suggests that NITESGON had a general memory enhancement effect. To test whether this memory enhancement effect stemmed (to some degree) from mitigating retrieval-induced forgetting, forgetting rates of these *original* vs *competing* stimuli were analysed for the two groups. Here, there was a significant large effect of stimuli ($F(1, 36) = 27.83$, $p < .001$, $\omega^2 = .176$), whereby from Day 1 to Day 2, *competing* pairs were forgotten (Active: M = −21.67, SD = 10.29; Sham: M = −25.00, SD = 13.38) more than *original* pairs (Active: M = −12.78, SD = 9.76; Sham: M = −13.00, SD = 10.93), regardless of group (see Fig. 5b). In addition, there was no significant effect of group ($F(1, 36) = 0.336$, $p = .565$, $\omega^2 = .000$). Thus, the results of these two analyses together novelly highlight how both groups forgot more *competing* pairs from Day 1 to Day 2. In other words, NITESGON had no impact on retrieval-induced forgetting, but rather it enhanced reconsolidation and retrieval of both *original* and *competing* pairs.

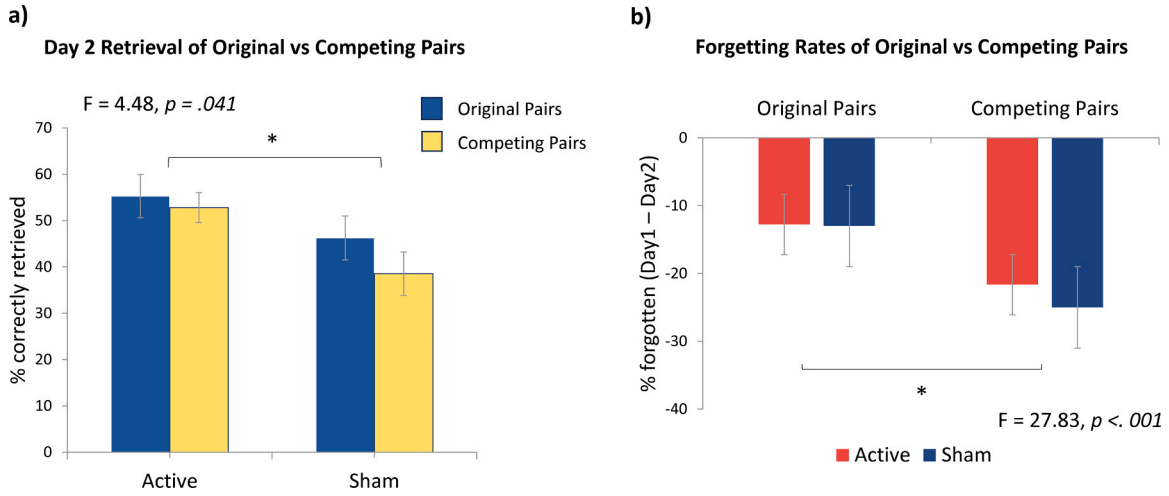

Fig. 5. Retrieval-induced Forgetting. a The active group retrieved significantly more *original* and *competing* pairs on Day 2 than the sham group. There was no significant difference in retrieval between the *original* and *competing* pairs, suggesting NITESGON had a general memory enhancement effect that may have stemmed from increased consolidation or downregulated retrieval-induced forgetting. **b** Given both active and sham groups forgot significantly more *competing* pairs than *original* pairs, this suggests that NITESGON had no impact on mitigating retrieval-induced forgetting of *competing* pairs.

3.2. Control measures

Between the active and sham NITESGON groups, there was no significant difference in their sex (χ^2 (1, N = 38) = .75, $p = .386$), gender (χ^2 (2, N = 38) = 1.01, $p = .604$), age (F (1, 36) = .04, $p = .838$, ω^2 = .000), handedness (χ^2 (1, N = 38) = .07, $p = .791$), or scores on the MMSE (F (1, 36) = 0.05, $p = .825$, ω^2 = .000), BDI (F (1, 36) = .03, $p = .859$, ω^2 = .000) or BAI (F (1, 36) = .02, $p = .886$, ω^2 = .000) measures. There was however a significant difference between groups in the hours of sleep on the night prior to participants' first day of participation (F (1, 36) = 5.10, $p = .030$, ω^2 = .097). However, while this was a moderate effect size, on average participants slept 7.35 h (Active: M = 6.9 h, SD =.71; Sham: M = 7.8 h, SD = 1.45). Furthermore, there was no significant difference between groups in the quality of sleep that night (χ^2 (7, N = 38) = 8.92, $p = .259$). Moreover, with regards to consolidation and stimulation effects, the hours and quality of sleep on the night between sessions was of more concern to the research question than the night prior to Session 1 (due to stimulation), and there were no significant differences between groups on quality of sleep (χ^2 (7, N = 38) = 12.58, $p = .083$) or hours of sleep (F (1, 36) = 2.24, $p = .143$, ω^2 = .032) on that night. See Table 1 for average scores of these measures for each group.

3.3. tES Exit Questionnaire

A MANOVA revealed a non-significant main effect of stimulation group (active vs sham) for the various tES side effects (Wilks' λ =.813, F (7, 30) = 0.99, $p = .458$) (See Fig. 6a). In particular, there were no measurable differences in scalp pain, neck pain or acute mood change symptoms, and no significant differences in the remaining symptoms (of headache, tingling, itching, burning, skin redness, sleepiness or trouble concentrating). All stimulation sessions were well tolerated, and no major stimulation related complications were noted. Blinding of stimulation conditions was effective as there was no significant difference between which groups participants thought they were in (active vs non-active) compared to their actual groups (active vs sham) (χ^2 (1, N = 38) = 1.79, $p = .180$) (see Fig. 6b). In the active group, 33.33% of participants believed they received the non-active stimulation, while 66.67% believed they received the active stimulation. In the sham group, 45% of participants thought they received the active stimulation, with the remaining 55% believing they received the sham stimulation.

4. Discussion

Reconsolidation refers to the process by which a previously consolidated memory, rendered labile upon retrieval, undergoes restabilisation. During this process, the memory can be strengthened further or become vulnerable to disruption. (Alberini & LeDoux, 2013; de Oliveira Alvares & Do-Monte, 2021; Lee et al., 2017; Sandrini et al., 2015; Sinclair & Barense, 2019). However, no prior research has investigated whether non-invasive peripheral nerve stimulation approaches can enhance memory by modulating these reconsolidation-stage processes. Thus, the main aims of this research were to investigate whether peripheral nerve stimulation could enhance reconsolidation, through boosting retrieval practice and/or mitigating retrieval-induced forgetting.

Firstly, results of this study show that NITESGON can strengthen memory reconsolidation via retrieval practice. To demonstrate this, *no-change* pairs were presented in Session 1 (during three encoding and retrieval phases). In Session 2, these same *no-change* pairs were presented (again during three encoding and retrieval phases, however with active or sham stimulation applied at the times of encoding). This session served as a reconsolidation phase for these stimuli, whereby the intention was to test whether stimulation could enhance reconsolidation of these pairs through retrieval practice. Memory retrieval for these pairs was then tested when participants returned on Day 2.

As expected, there were no significant differences between active and sham groups in learning of the *no-change* pairs on Session 1, confirming equivalent learning pre-stimulation. However, there were significant differences between the groups at the reconsolidation stage in Session 2, and when memory was tested 24 h later, with the active group retrieving more *no-change* pairs at both time points than the sham group. These results highlight how peripheral nerve stimulation can bolster reconsolidation leading to sustained memory benefits 24 h later. It is important to emphasise how the *no-change* pairs were the only list of pairs in Session 2 where there was a significant difference between groups (see Table 2), and which had already been presented in Session 1. In other words, this effect was not observed for newly introduced material in Session 2. Thus, this novelly highlights how during reconsolidation, peripheral nerve stimulation applied at the time of studying previously-consolidated information, strengthens retrieval practice, and leads to sustained memory retrieval. These findings align with the idea that reactivated memories enter a transiently plastic state during which NITESGON appears to have amplified the strengthening effect typically produced by retrieval practice, leading to sustained memory

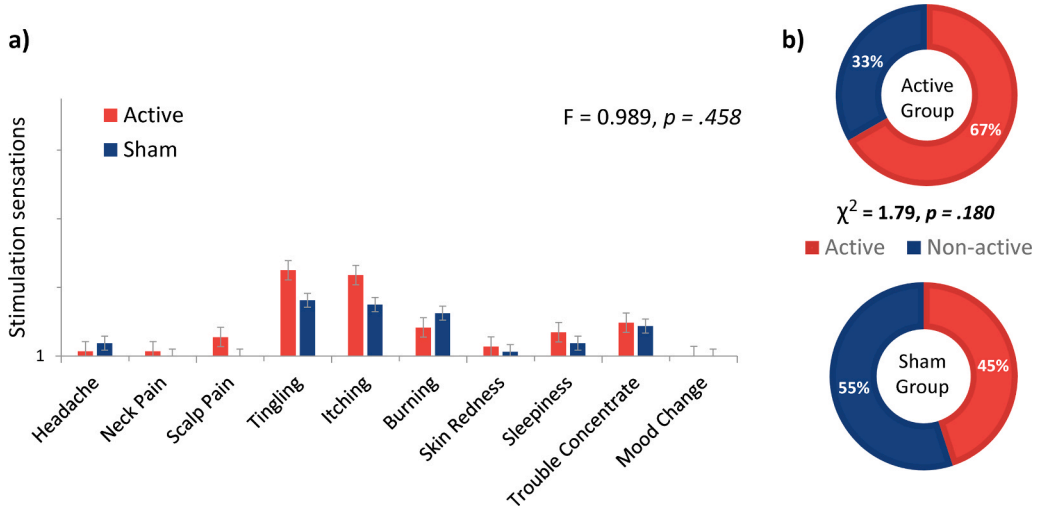

Fig. 6. Stimulation Sensations and Stimulation Blinding. a There were no measurable differences between active and sham stimulation for neck pain, scalp pain and mood change stimulation sensations, and no significant differences found between active and sham stimulation for the remaining stimulation sensations. **b** There was no significant difference found between the stimulation that participants received (active/ sham) versus what they believed they received (active/ non-active).

benefits observed 24 h later.

At the time of reconsolidation, memories are rendered labile - meaning they can either be further strengthened or are likewise sensitive to disruption (Alberini & LeDoux, 2013; Lee et al., 2017; Sandrini et al., 2015). Furthermore, the act of retrieval can both support the maintenance of certain memories or induce forgetting of others (Hulbert & Anderson, 2020; Murayama et al., 2014). Thus, the second aim of this research was to investigate whether peripheral nerve stimulation could modulate retrieval-induced forgetting.

To investigate this, participants first learned *original* cue-target pairs in Session 1. In Session 2, the same cues were paired with *competing* targets under active or sham stimulation. On Day 2, memory retrieval for both *original* and *competing* pairs was assessed. Indeed, on Day 2, although the active group showed overall better memory than the sham group, forgetting rates did not differ between groups. Across participants, *competing* pairs were forgotten more than *original* pairs, demonstrating a typical retrieval-induced forgetting pattern. However, stimulation did not reduce or exacerbate this effect. These findings indicate that NITESGON did not influence reconsolidation by altering inhibitory processes that suppress competing memories. Instead, its effects appear to reflect memory strengthening mechanisms rather than modulation of forgetting.

This dissociation is theoretically informative. Retrieval-induced forgetting is thought to arise from prefrontal inhibitory control processes that suppress competing memory traces (Levy & Anderson, 2002; Wimber et al., 2015; Wimber et al., 2008). In contrast, reconsolidation-related strengthening is more closely linked to hippocampal plasticity mechanisms (Kim et al., 2021; Osorio-Gómez et al., 2023; Schroeder et al., 2023). The present results therefore may suggest that peripheral nerve stimulation preferentially influenced hippocampal–memory stabilisation processes rather than prefrontal inhibitory control mechanisms.

These findings extend previous work demonstrating that NITESGON selectively enhances consolidation but not acquisition, retrieval, or forgetting (Luckey et al., 2022; Vanneste et al., 2020). The present study identifies reconsolidation as an additional memory stage sensitive to this form of peripheral nerve stimulation. Importantly, the absence of effects on retrieval-induced forgetting is consistent with earlier findings showing that NITESGON does not alter forgetting rates in older adults (Luckey et al., 2020), reinforcing the view that its effects are stage-specific rather than global.

In terms of the putative mechanism behind this neurostimulation approach, originally, non-invasive neurostimulation approaches employing tDCS or transcranial alternating current stimulation (tACS) were applied to the head with the aim of modulating brain activity and influencing behaviour (Woods et al., 2016). However, in recent years, research continues to build highlighting how these neurostimulation approaches can exert their effects not only through direct *transcranial* pathways to the brain, but also through indirect *transcutaneous* peripheral nerve pathways (Asamoah et al., 2019; van Boekholdt et al., 2021; Vöröslakos et al., 2018). These peripheral nerves include the vagus nerve, trigeminal nerve and greater occipital nerve. This peripheral nerve route to modulating memory has been validated by prior research (L. Chen, Sun, et al., 2025; Clark et al., 1999; Jacobs et al., 2015; Luckey et al., 2023). In this transcutaneous route, when stimulation is applied non-invasively to the head or neck, peripheral nerves located just under the skin are argued to receive a greater proportion of the electrical current stimulation than deeper brain regions located beneath the skull (van Boekholdt et al., 2021).

Indeed, in rodents, peripheral nerve stimulation has been shown to activate deep brain regions such as the hippocampus or brainstem nuclei (L. Chen et al., 2025; Hulsey et al., 2017), and blocking these peripheral nerve routes subsequently blocks brainstem nuclei activity in response to stimulation (Majdi et al., 2025). This highlights how these peripheral nerve pathways behind transcutaneous stimulation are essential in activating deeper brain regions (Luckey et al., 2023; Majdi et al., 2024). Furthermore, neurotransmitter activity has been implicated in the mechanism(s) through which these peripheral nerves have been shown to modulate brain activity, support synaptic plasticity processes and influence cognitive, memory and motor function (Asamoah et al., 2019; Hulsey et al., 2016; Hulsey et al., 2019; Luckey et al., 2023; Luckey et al., 2022). Specifically, research conducted by our lab on stimulating the greater occipital nerve has demonstrated that NITESGON supports consolidation and retention of memories through a locus coeruleus-noradrenaline pathway that facilitates hippocampal activation (Luckey, McLeod, et al., 2023; Vanneste et al., 2020).

Thus, in light of the above literature, in this present study, it is postulated that NITESGON strengthens existing memories by upregulating neuromodulatory input to hippocampal circuits during memory reactivation. This interpretation is consistent with prior demonstrations that NITESGON increases markers of locus coeruleus–noradrenaline and dopaminergic activity (Luckey, McLeod, et al., 2023; Vanneste et al., 2020), both of which are known to facilitate synaptic plasticity and memory stabilisation (Hansen, 2017). However, given that the present study did not include direct neurophysiological measurements, future research is warranted to confirm whether this same mechanism (or others) underlie NITESGON's effects on reconsolidation.

In parallel, forgetting is not a passive process, but involves active inhibition mediated by medial prefrontal and dorsolateral prefrontal cortical regions on downstream hippocampal memory traces (Levy & Anderson, 2002; Wimber et al., 2015; Wimber et al., 2008). Moreover, dopamine is reported to play a critical role in prefrontal inhibitory control during retrieval-induced forgetting (Berry et al., 2024; Castillo Díaz et al., 2021; Gallo et al., 2022; Wimber et al., 2011). Thus, the absence of NITESGON's effect on retrieval-induced forgetting is notable. One possibility is that NITESGON's neuromodulatory effects are biased toward hippocampal and brainstem pathways rather than prefrontal control networks. This compares to a recent neurostimulation study which demonstrated that disrupting prefrontal activity can reduce retrieval-induced forgetting. In that study, high-definition tDCS over the medial prefrontal cortex decreased forgetting of competing memories by altering inhibitory control signals (Khan et al., 2024). Specifically, in response to stimulation, beta desynchronization in fronto-parietal networks during retrieval practice was associated with stronger suppression of competitors, suggesting dynamic communication changes as inhibitory processes unfold.

Following this logic, NITESGON may enhance memory strengthening without substantially influencing the top-down inhibitory mechanisms required for adaptive forgetting. Indeed, prior studies by our lab have demonstrated how NITESGON increases activity in hippocampal regions and specifically theta-gamma coupling in medial temporal cortical regions (Luckey et al., 2023; Vanneste et al., 2020), which is widely acknowledged as a core mechanism for memory processing enabling the encoding, retrieval and organisation of information in time (Colgin, 2015; Jensen & Colgin, 2007; Köster et al., 2014). However, future research combining NITESGON with neuroimaging will be required to confirm whether this mechanism contributes to the present results.

Interestingly, contemporary perspectives suggest that predictive coding serves as a core computational model for memory updating and retrieval, where the brain constantly generates hierarchical predictions and uses prediction error to determine whether a memory should be updated or suppressed (Bayer et al., 2025; de Oliveira Alvares & Do-Monte, 2021; Sinclair & Barense, 2019; Vaverková et al., 2020). According to the predictive coding viewpoint, the brain constantly forms predictions about memory content based on prior experience and uses prediction errors (mismatches between expected and actual inputs) to decide whether or not to destabilise existing memories for reconsolidation or suppress competing memories (Sinclair & Barense, 2019). Theta–gamma coupling in hippocampal–cortical networks has been proposed as a mechanism supporting this updating process (Köster, 2024; Köster & Gruber, 2022), while neuromodulators from the locus

coeruleus such as noradrenaline and dopamine signal the salience of prediction errors (Groves et al., 2025).

In parallel, NITESGON has previously been associated with increased hippocampal activity and enhanced theta–gamma coupling (Luckey et al., 2023; Vanneste et al., 2020), raising the possibility that stimulation amplified neural dynamics supporting prediction-error-driven memory updating. In contrast, retrieval-induced forgetting is more closely linked to beta-band activity in prefrontal control networks associated with inhibitory suppression of competing traces (Khan et al., 2024). The present dissociation between enhanced reconsolidation and unchanged retrieval-induced forgetting is therefore consistent with the notion that NITESGON primarily influenced prediction-error–driven updating mechanisms rather than inhibitory control processes, although this remains to be directly tested.

When interpreting the current findings, it is important to consider the limitations that exist within the research. Although some of the significant findings here involve large effect sizes, others range from small to moderate effect sizes. Thus, while these findings provide initial support for how peripheral nerve stimulation can support reconsolidation processes, additional research should validate these claims. In line with this, in addition to the analyses included in the supplementary materials, to further verify the existence of the reconsolidation effect (and to rule out general neurostimulation effects as an alternative explanation of the results in the present study), future research could also include a no-retrieval/ stimulation-only control group for comparison, whereby no learning occurs in Session 2, and only NITESGON is applied. Additionally, the study's sample consisted of young healthy individuals, as such the generalisability of the findings need to be confirmed with future research. This is especially the case in order to investigate the potential translational applicability of these results.

For example, given that reconsolidation processes involving retrieval practice or retrieval-induced forgetting are implicated in conditions such as schizophrenia or prodromal stages of Alzheimer's disease (Ebert & Anderson, 2009; Hanseeuw et al., 2012; Jantzi et al., 2019), the ability to modulate these processes may have clinical applications, but next steps should firstly include additional validation of these neurostimulation results. Additionally, reconsolidation-based interventions have been widely studied in conditioned fear and cue-reactivity models relevant to PTSD (Astill Wright et al., 2021; Noël, 2023), and behavioural reconsolidation modification procedures are being investigated for reducing cue-induced craving in addiction models or substance use disorders (B. Chen, Sun, et al., 2025; Yue et al., 2025). However, less is known about whether declarative memory components of these disorders can be similarly updated (Kim et al., 2021). The present findings may therefore be particularly relevant for understanding how stimulation could influence reconsolidation of hippocampal-dependent associative memories, such as autobiographical or contextual elements linked to traumatic or substance-related experiences. Thus, investigating these questions will not only help with our mechanistic understanding of peripheral nerve stimulation's impact on memory processes, but also may outline future therapeutic avenues worth investigating.

5. Conclusion

This study provides novel evidence that peripheral nerve stimulation via tDCS of the greater occipital nerve enhances memory reconsolidation through retrieval practice, but does not mitigate retrieval-induced forgetting. These findings clarify the stage-specific effects of peripheral nerve stimulation on memory, indicating that its benefits arise from strengthening reconsolidation rather than reducing interference. In addition, the findings validate prior research by confirming that this stimulation approach supports consolidation, but not acquisition or forgetting processes. Beyond advancing mechanistic understanding, this preliminary work suggests the potential translational relevance of peripheral nerve stimulation for disorders marked by memory dysfunction such as Alzheimer's, as well as PTSD or addiction-related disorders.

CRediT authorship contribution statement

Sven Vanneste: Writing – original draft, Supervision, Methodology, Funding acquisition, Conceptualization. **Caledonia Steltzner:** Investigation, Data curation. **Elva Arulchelvan:** Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

AI was not used in writing the paper

Declaration of Competing Interest

The authors have no conflicts of interest

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.biopsycho.2026.109229.

Data availability

Data will be made available on request.

References

Alberini, C. M., & LeDoux, J. E. (2013). Memory reconsolidation. *Current Biology, 23*(17), R746–R750. https://doi.org/10.1016/j.cub.2013.06.046

Anderson, M. C., Bjork, R. A., & Bjork, E. L. (1994). Remembering can cause forgetting: Retrieval dynamics in long-term memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 20*(5), 1063–1087. https://doi.org/10.1037//0278-7393.20.5.1063

Anderson, M. C., & Neely, J. H. (1996). Chapter 8 - Interference and Inhibition in Memory Retrieval. In E. L. Bjork, & R. A. Bjork (Eds.), *Memory* (pp. 237–313). Academic Press. https://doi.org/10.1016/B978-012102570-0/50010-0.

Asamoah, B., Khatoun, A., & Mc Laughlin, M. (2019). tACS motor system effects can be caused by transcutaneous stimulation of peripheral nerves. *Nature Communications, 10*(1), 266. https://doi.org/10.1038/s41467-018-08183-w

Astill Wright, L., Horstmann, L., Holmes, E. A., & Bisson, J. I. (2021). Consolidation/reconsolidation therapies for the prevention and treatment of PTSD and re-experiencing: A systematic review and meta-analysis. *Translational Psychiatry, 11*(1), 453. https://doi.org/10.1038/s41398-021-01570-w

Bardhoshi, G., Duncan, K., & Erford, B. T. (2016). Psychometric meta-analysis of the english version of the beck anxiety inventory. *Journal of Counseling & Development, 94*(3), 356–373. https://doi.org/10.1002/jcad.12090

Bayer, H., Bertoglio, L. J., Maren, S., & Stern, C. A. J. (2025). Windows of change: Revisiting temporal and molecular dynamics of memory reconsolidation and persistence. *Neuroscience & Biobehavioral Reviews, 174*, Article 106198. https://doi.org/10.1016/j.neubiorev.2025.106198

Berry, J. A., Guhle, D. C., & Davis, R. L. (2024). Active forgetting and neuropsychiatric diseases. *Molecular Psychiatry, 29*(9), 2810–2820. https://doi.org/10.1038/s41380-024-02521-9

Brunoni, A. R., Amadera, J., Berbel, B., Volz, M. S., Rizzerio, B. G., & Fregni, F. (2011). A systematic review on reporting and assessment of adverse effects associated with transcranial direct current stimulation. *International Journal of Neuropsychopharmacology, 14*(8), 1133–1145. https://doi.org/10.1017/s1461145710001690

Castillo Díaz, F., Caffino, L., & Fumagalli, F. (2021). Bidirectional role of dopamine in learning and memory-active forgetting. *Neuroscience & Biobehavioral Reviews, 131*, 953–963. https://doi.org/10.1016/j.neubiorev.2021.10.011

Chen, B., Gan, H., Yang, L., Yan, X., Lv, X., Zhang, X., & Bu, J. (2025). A novel imagery-based retrieval-extinction training for intervention in nicotine addiction. *BMC Medicine, 23*(1), 568. https://doi.org/10.1186/s12916-025-04386-3

Chen, L., Sun, Q., Seminck, N., Huang, H., Asamoah, B., & Laughlin, M. M. (2025). Investigating the effect of non-invasive trigeminal nerve stimulation on memory consolidation: Insights from animal and human studies. *Brain Stimulation: Basic, Translational, and Clinical Research in Neuromodulation, 18*(1), 487. https://doi.org/10.1016/j.brs.2024.12.795

Clark, K. B., Naritoku, D. K., Smith, D. C., Browning, R. A., & Jensen, R. A. (1999). Enhanced recognition memory following vagus nerve stimulation in human subjects. *Nature Neuroscience, 2*(1), 94–98. https://doi.org/10.1038/4600

Colgin, L. L. (2015). Theta-gamma coupling in the entorhinal-hippocampal system. *Current Opinion in Neurobiology, 31*, 45–50. https://doi.org/10.1016/j.conb.2014.08.001

de Oliveira Alvares, L., & Do-Monte, F. H. (2021). Understanding the dynamic and destiny of memories. *Neuroscience & Biobehavioral Reviews, 125*, 592–607. https://doi.org/10.1016/j.neubiorev.2021.03.009

Ebert, P. L., & Anderson, N. D. (2009). Proactive and retroactive interference in young adults, healthy older adults, and older adults with amnestic mild cognitive impairment. *Journal of the International Neuropsychological Society, 15*(1), 83–93. https://doi.org/10.1017/S1355617708090115

Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2009). Statistical power analyses using G*Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods, 41*(4), 1149–1160. https://doi.org/10.3758/BRM.41.4.1149

Gallo, F. T., Zanoni Saad, M. B., Silva, A., Morici, J. F., Miranda, M., Anderson, M. C., Weisstaub, N. V., & Bekinschtein, P. (2022). Dopamine modulates adaptive forgetting in medial prefrontal cortex. *Journal of Neuroscience, 42*(34), 6620–6636. https://doi.org/10.1523/jneurosci.0740-21.2022

Goadsby, P. J., Bartsch, T., & Dodick, D. W. (2008). Occipital nerve stimulation for headache: Mechanisms and efficacy. *Headache: The Journal of Head and Face Pain, 48*(2), 313–318. https://doi.org/10.1111/j.1526-4610.2007.01022.x

Groves, I., Grella, S. L., Harley, C. W., Hardt, O., & Nadel, L. (2025). How prediction error drives memory updating: role of locus coeruleus–hippocampal interactions. *Trends in Neurosciences, 48*(11), 865–876. https://doi.org/10.1016/j.tins.2025.09.003

Hanseeuw, B. J., Seron, X., & Ivanoiu, A. (2012). Increased sensitivity to proactive and retroactive interference in amnestic mild cognitive impairment: New insights. *Brain and Cognition, 80*(1), 104–110. https://doi.org/10.1016/j.bandc.2012.04.002

Hansen, N. (2017). The longevity of hippocampus-dependent memory is orchestrated by the locus coeruleus-noradrenergic system. *Neural Plasticity, 2017*, Article 2727602. https://doi.org/10.1155/2017/2727602

Haubrich, J., Bernabo, M., & Nader, K. (2020). Noradrenergic projections from the locus coeruleus to the amygdala constrain fear memory reconsolidation. *eLife, 9*. https://doi.org/10.7554/eLife.57010

Hulbert, J. C., & Anderson, M. C. (2020). Does retrieving a memory insulate it against memory inhibition? A retroactive interference study. *Memory, 28*(3), 293–308. https://doi.org/10.1080/09658211.2019.1710216

Hulsey, D. R., Hays, S. A., Khodaparast, N., Ruiz, A., Das, P., Rennaker, R. L., & Kilgard, M. P. (2016). Reorganization of Motor Cortex by Vagus Nerve Stimulation Requires Cholinergic Innervation. *Brain Stimulation, 9*(2), 174–181. https://doi.org/10.1016/j.brs.2015.12.007

Hulsey, D. R., Riley, J. R., Loerwald, K. W., Rennaker, R. L., Kilgard, M. P., & Hays, S. A. (2017). Parametric characterization of neural activity in the locus coeruleus in response to vagus nerve stimulation. *Experimental Neurology, 289*, 21–30. https://doi.org/10.1016/j.expneurol.2016.12.005

Hulsey, D. R., Shedd, C. M., Sarker, S. F., Kilgard, M. P., & Hays, S. A. (2019). Norepinephrine and serotonin are required for vagus nerve stimulation directed cortical plasticity. *Experimental Neurology, 320*, Article 112975. https://doi.org/10.1016/j.expneurol.2019.112975

Jacobs, H. I., Riphagen, J. M., Razat, C. M., Wiese, S., & Sack, A. T. (2015). Transcutaneous vagus nerve stimulation boosts associative memory in older individuals. *Neurobiol Aging, 36*(5), 1860–1867. https://doi.org/10.1016/j.neurobiolaging.2015.02.023

Jantzi, C., Mengin, A. C., Serfaty, D., Bacon, E., Elowe, J., Severac, F., Meyer, N., Berna, F., & Vidailhet, P. (2019). Retrieval practice improves memory in patients with schizophrenia: New perspectives for cognitive remediation. *BMC Psychiatry, 19*(1), 355. https://doi.org/10.1186/s12888-019-2341-y

Jensen, O., & Colgin, L. L. (2007). Cross-frequency coupling between neuronal oscillations. *Trends in Cognitive Sciences, 11*(7), 267–269. https://doi.org/10.1016/j.tics.2007.05.003

Karpicke, J. D., & Roediger, H. L., 3rd (2008). The critical importance of retrieval for learning. *Science, 319*(5865), 966–968. https://doi.org/10.1126/science.1152408

Khan, A., Ti, C. H. E., Yuan, K., Crespo Garcia, M., Anderson, M. C., & Tong, R. K.-Y. (2024). Medial Prefrontal Cortex Stimulation Reduces Retrieval-Induced Forgetting via Fronto-parietal Beta Desynchronization. *The Journal of Neuroscience, 44*(37), Article e0189242024. https://doi.org/10.1523/jneurosci.0189-24.2024

Kim, G., Kwon, M., Kang, W., & Lee, S. H. (2021). Is Reconsolidation a general property of memory? *Frontiers in Human Neuroscience, 15*, Article 643106. https://doi.org/10.3389/fnhum.2021.643106

Köster, M. (2024). The theta-gamma code in predictive processing and mnemonic updating. *Neuroscience & Biobehavioral Reviews, 158*, Article 105529. https://doi.org/10.1016/j.neubiorev.2023.105529

Köster, M., Friese, U., Schöne, B., Trujillo-Barreto, N., & Gruber, T. (2014). Theta–gamma coupling during episodic retrieval in the human EEG. *Brain Research, 1577*, 57–68. https://doi.org/10.1016/j.brainres.2014.06.028

Köster, M., & Gruber, T. (2022). Rhythms of human attention and memory: An embedded process perspective [Review]. *Frontiers in Human Neuroscience, 16*, *2022*. https://doi.org/10.3389/fnhum.2022.905837

Lee, J. L. C., Nader, K., & Schiller, D. (2017). An Update on Memory Reconsolidation Updating. *Trends in Cognitive Sciences, 21*(7), 531–545. https://doi.org/10.1016/j.tics.2017.04.006

Levy, B. J., & Anderson, M. C. (2002). Inhibitory processes and the control of memory retrieval. *Trends in Cognitive Sciences, 6*(7), 299–305. https://doi.org/10.1016/S1364-6613(02)01923-X

Luckey, A. M., Adcock, K., & Vanneste, S. (2023). Peripheral nerve stimulation: A neuromodulation-based approach. *Neuroscience & Biobehavioral Reviews, 149*, Article 105180. https://doi.org/10.1016/j.neubiorev.2023.105180

Luckey, A. M., McLeod, L. S., Huang, Y., Mohan, A., & Vanneste, S. (2023). Making memories last using the peripheral effect of direct current stimulation. *eLife, 12*, Article e75586. https://doi.org/10.7554/eLife.75586

Luckey, A. M., McLeod, S. L., Mohan, A., & Vanneste, S. (2022). Potential role for peripheral nerve stimulation on learning and long-term memory: A comparison of alternating and direct current stimulations. *Brain Stimulation: Basic, Translational, and Clinical Research in Neuromodulation, 15*(3), 536–545. https://doi.org/10.1016/j.brs.2022.03.001

Luckey, A. M., McLeod, S. L., Robertson, I. H., To, W. T., & Vanneste, S. (2020). Greater occipital nerve stimulation boosts associative memory in older individuals: A randomized trial. *Neurorehabil Neural Repair, 34*(11), 1020–1029. https://doi.org/10.1177/1545968320943573

Majdi, A., Asamoah, B., & Mc Laughlin, M. (2024). Understanding novel neuromodulation pathways in tDCS: brain stem recordings in rats during trigeminal nerve direct current stimulation. *Translational Psychiatry, 14*(1), 456. https://doi.org/10.1038/s41398-024-03158-6

Majdi, A., Chen, L., Larsen, L. E., Raedt, R., & Laughlin, M. M. (2025). tDCS cranial nerve Co-stimulation: Unveiling brainstem pathways involved in trigeminal nerve direct current stimulation in rats. *Brain Stimulation, 18*(2), 171–184. https://doi.org/10.1016/j.brs.2025.01.025

Miller, R. R. (2021). Failures of memory and the fate of forgotten memories. *Neurobiology of Learning and Memory, 181*, Article 107426. https://doi.org/10.1016/j.nlm.2021.107426

Mitchell, A. J. (2017). The Mini-Mental State Examination (MMSE): Update on its diagnostic accuracy and clinical utility for cognitive disorders. In A. J. Larner (Ed.), *Cognitive Screening Instruments: A Practical Approach* (pp. 37–48). Springer International Publishing. https://doi.org/10.1007/978-3-319-44775-9_3.

Murayama, K., Miyatsu, T., Buchli, D., & Storm, B. C. (2014). Forgetting as a consequence of retrieval: a meta-analytic review of retrieval-induced forgetting. In *Psychol Bull, 140* pp. 1383–1409). https://doi.org/10.1037/a0037505

Nader, K. (2015). Reconsolidation and the dynamic nature of memory. *Cold Spring Harb Perspect Biology, 7*(10), a021782. https://doi.org/10.1101/cshperspect.a021782

Nelson, T. O., & Dunlosky, J. (1994). Norms of paired-associate recall during multitrial learning of Swahili-english translation equivalents. *Memory, 2*(3), 325–335. https://doi.org/10.1080/09658219408258951

Noël, X. (2023). A critical perspective on updating drug memories through the integration of memory editing and brain stimulation [Mini Review]. *Frontiers in Psychiatry, 14*. https://doi.org/10.3389/fpsyt.2023.1161879

Osorio-Gómez, D., Miranda, M. I., Guzmán-Ramos, K., & Bermúdez-Rattoni, F. (2023). Transforming experiences: Neurobiology of memory updating/editing. *Frontiers in Systems Neuroscience, 17*, Article 1103770. https://doi.org/10.3389/fnsys.2023.1103770

Pigeon, S., Lonergan, M., Rotondo, O., Pitman, R. K., & Brunet, A. (2022). Impairing memory reconsolidation with propranolol in healthy and clinical samples: A meta-analysis. *Journal of Psychiatry and Neuroscience, 47*(2), E109–E122. https://doi.org/10.1503/jpn.210057

Roediger, H. L., III, & Butler, A. C. (2011). The critical role of retrieval practice in long-term retention. *Trends in Cognitive Sciences, 15*(1), 20–27. https://doi.org/10.1016/j.tics.2010.09.003

Sandrini, M., Cohen, L. G., & Censor, N. (2015). Modulating reconsolidation: a link to causal systems-level dynamics of human memories. *Trends in Cognitive Sciences, 19*(8), 475–482. https://doi.org/10.1016/j.tics.2015.06.002

Sara, S. J. (2009). The locus coeruleus and noradrenergic modulation of cognition. *Nature Reviews Neuroscience, 10*(3), 211–223. https://doi.org/10.1038/nrn2573

Schroeder, M. N., Fullio, C. L., Ballarini, F., & Moncada, D. (2023). Modulation of memory reconsolidation by adjacent novel tasks: timing defines the nature of change. *Communications Biology, 6*(1), 1288. https://doi.org/10.1038/s42003-023-05666-5

Sinclair, A. H., & Barense, M. D. (2019). Prediction error and memory reactivation: How incomplete reminders drive reconsolidation. *Trends in Neurosciences, 42*(10), 727–739. https://doi.org/10.1016/j.tins.2019.08.007

Squire, L. R., Genzel, L., Wixted, J. T., & Morris, R. G. (2015). Memory consolidation. *Cold Spring Harb Perspect Biology, 7*(8), a021766. https://doi.org/10.1101/cshperspect.a021766

Tronson, N. C., & Taylor, J. R. (2007). Molecular mechanisms of memory reconsolidation. *Nature Reviews Neuroscience, 8*(4), 262–275. https://doi.org/10.1038/nrn2090

van Boekholdt, L., Kerstens, S., Khatoun, A., Asamoah, B., & Mc Laughlin, M. (2021). tDCS peripheral nerve stimulation: a neglected mode of action? *Molecular Psychiatry, 26*(2), 456–461. https://doi.org/10.1038/s41380-020-00962-6

Vanneste, S., Mohan, A., Yoo, H. B., Huang, Y., Luckey, A. M., McLeod, S. L., Tabet, M. N., Souza, R. R., McIntyre, C. K., Chapman, S., Robertson, I. H., & To, W. T. (2020). The peripheral effect of direct current stimulation on brain circuits involving memory. *Science Advances, 6*(45), Article eaax9538. https://doi.org/10.1126/sciadv.aax9538

Vaverková, Z., Milton, A. L., & Merlo, E. (2020). Retrieval-dependent mechanisms affecting emotional memory persistence: Reconsolidation, extinction, and the space in between [Review]. *Frontiers in Behavioral Neuroscience, 14*, *2020*. https://doi.org/10.3389/fnbeh.2020.574358

Vöröslakos, M., Takeuchi, Y., Brinyiczki, K., Zombori, T., Oliva, A., Fernández-Ruiz, A., Kozák, G., Kincses, Z. T., Iványi, B., Buzsáki, G., & Berényi, A. (2018). Direct effects of transcranial electric stimulation on brain circuits in rats and humans. *Nature Communications, 9*(1), 483. https://doi.org/10.1038/s41467-018-02928-3

Whisman, M. A., & Richardson, E. D. (2015). Normative data on the beck depression inventory – Second edition (BDI-II) in college students. *Journal of Clinical Psychology, 71*(9), 898–907. https://doi.org/10.1002/jclp.22188

Wimber, M., Alink, A., Charest, I., Kriegeskorte, N., & Anderson, M. C. (2015). Retrieval induces adaptive forgetting of competing memories via cortical pattern suppression. *Nature Neuroscience, 18*(4), 582–589. https://doi.org/10.1038/nn.3973

Wimber, M., Bäuml, K.-H., Bergström, Z., Markopoulos, G., Heinze, H.-J., & Richardson-Klavehn, A. (2008). Neural markers of inhibition in human memory retrieval. *The*

Journal of Neuroscience, 28(50), 13419–13427. https://doi.org/10.1523/jneurosci.1916-08.2008

Wimber, M., Schott, B. H., Wendler, F., Seidenbecher, C. I., Behnisch, G., Macharadze, T., Bäuml, K. H. T., & Richardson-Klavehn, A. (2011). Prefrontal dopamine and the dynamic control of human long-term memory. e15-e15 *Translational Psychiatry, 1*(7). https://doi.org/10.1038/tp.2011.15.

Woods, A. J., Antal, A., Bikson, M., Boggio, P. S., Brunoni, A. R., Celnik, P., Cohen, L. G., Fregni, F., Herrmann, C. S., Kappenman, E. S., Knotkova, H., Liebetanz, D., Miniussi, C., Miranda, P. C., Paulus, W., Priori, A., Reato, D., Stagg, C., Wenderoth, N., & Nitsche, M. A. (2016). A technical guide to tDCS, and related non-invasive brain stimulation tools. *Clinical Neurophysiology, 127*(2), 1031–1048. https://doi.org/10.1016/j.clinph.2015.11.012

Yue, J.-L., Wang, R.-J., Chen, S.-J., Lin, X., Fang, Q., Guo, X.-J., Sun, Y.-K., Yuan, K., Bao, Y.-P., Shi, J., Xue, Y.-X., Wu, P., & Lu, L. (2025). Effect of conditioned stimuli-triggered memory retrieval-extinction in patients with methamphetamine use disorder. *Translational Psychiatry, 15*(1), 249. https://doi.org/10.1038/s41398-025-03474-5