

Transcranial direct current stimulation over the left posterior temporal lobe modulates semantic control: Evidence from episodic memory distortions

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ABSTRACT

Evidence accumulates to show that semantic cognition requires, in addition to semantic representations, control processes that regulate the accessibility and use of semantic knowledge in a task- and time-appropriate fashion. Semantic control has been recently proposed to rely on a distributed network that includes the posterior temporal cortex. Along these lines, recent *meta*-analyses of neuroimaging data and studies with patients suffering from semantic aphasia have suggested that the left posterior middle temporal gyrus (pMTG) is critically involved whenever situational context must constrain semantic retrieval. In the present experiment, we used transcranial direct current stimulation over the left posterior temporal lobe in an attempt to interfere with semantic control while participants performed a DRM task, a procedure for inducing conceptually-based false recognition that is contingent on both activation and control processes. Paralleling findings with patients suffering from brain damage restricted to the temporoparietal cortex, anodal stimulation (relative to sham stimulation) resulted in increased false recognition but intact true recognition. These findings fit well with the idea that the left pMTG is a key component of a semantic control network, the alteration of which results in memory performance that is affected by the intrusion of contextually-inappropriate semantic information.

1. Introduction

Over the last years, studies using a variety of methodological approaches have provided compelling evidence that semantic cognition requires a combination of two interacting components: semantic representations and control processes. Briefly stated, semantic representations underpin the capacity to create and maintain conceptual knowledge from multimodal (verbal and non-verbal) experiences, whereas control processes regulate the accessibility and use of semantic representations in a task- and time-appropriate fashion (Jefferies & Lambon Ralph, 2006; Noonan et al., 2010, 2013). This control function, a means of bringing purpose and flexibility to semantically imbued behavior, is as crucial as the availability of a representational knowledge base because, in many different situations, focusing on some aspects of meaning and ignoring others is of capital importance.

A brain region that has shown to be critically involved in the formation and maintenance of complex semantic representations is the anterior temporal lobe (ATL), which is thought to serve as an integration

hub in charge of binding together modality-specific information from distributed cortices to create coherent conceptual representations (Bonner & Price, 2013; Díez et al., 2017; Lambon Ralph, 2014; Wong & Gallate, 2012). In contrast, semantic control has been traditionally associated with ventrolateral regions of the prefrontal cortex, and more specifically the inferior frontal gyrus (IFG) (Badre et al., 2005; Dudukovic & Kuhl, 2017; Thompson-Schill et al., 1997). It has also been suggested that this control function over semantic representations might rely on a wider distributed network that additionally includes the posterior temporal and parietal cortices (Jefferies & Lambon Ralph, 2006; Noonan et al., 2013; Thompson et al., 2022; Whitney, Jefferies, et al., 2011). Both left and right brain regions contribute to these two aspects of semantic cognition but, as further described in what follows, much of the involved structures and networks are strongly left-lateralized (Gonzalez Alam et al., 2019; Hodgson et al., 2022).

A wealth of neuropsychology data involving comparisons of patients with different patterns of brain damage supports the distinction between representation and control components in semantic cognition. As an

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example, while patients with semantic dementia (SD), who typically suffer bilateral damage in the ATL, may be characterized by exhibiting degraded semantic knowledge, such as difficulties in naming pictures of common objects (Hodges & Patterson, 1997), patients with semantic aphasia (SA) show greater problems in semantic access under conditions that impose high demands of control, as when attempting to retrieve aspects of knowledge that are not the dominant response to the inputs provided (Noonan et al., 2010). Interestingly, SA patients present damage either in the IFG or in the posterior middle temporal gyrus (pMTG), or both (Jefferies & Lambon Ralph, 2006).

Converging evidence characterizing the representation and control systems, as well as evidence of the dissociation between them in semantic cognition tasks, comes from several neuroimaging and neuro-modulation studies, at times combining both types of techniques (Binney et al., 2010; Pobric et al., 2010; Rice et al., 2015; Visser & Lambon Ralph, 2011). Of particular relevance here, a number of fMRI studies using a variety of semantic tasks have shown that both the IFG and the pMTG (especially in the left hemisphere) become more activated under experimental conditions with higher control requirements (see meta-analyses by Jackson, 2021, and by Noonan et al., 2013). And repetitive transcranial magnetic stimulation (rTMS) on either the left IFG or pMTG produces semantic impairments that are only noticeable in executive demanding tasks (Davey et al., 2015; Hoffman et al., 2010; Whitney, Kirk, et al., 2011).

It is worth mentioning that the multiple brain regions identified by neuroimaging and brain stimulation studies largely overlap with the most damaged areas in SA patients, an observation that has recently served as ground to argue that semantic control is subserved by a left-focused distributed network, including the PFC, the angular gyrus and the pMTG (Jackson, 2021; Noonan et al., 2013). Further support for the implication of the left pMTG in this large-scale network of semantic control comes from a recent study that combined analyses of MRI-based cortical thickness with fMRI connectivity at rest to identify structural markers of individual differences in semantic control (Wang et al., 2018). In this study, participants with better performance on a controlled semantic retrieval task exhibited increased structural covariance between the left pMTG and the left PFC. This covariance, however, was not found with performance in harder but non-semantic tasks, which suggests it is specific to semantic control. Also, an fMRI study by Davey et al. (2016) suggests that the left pMTG, together with the anterior ventral IFG, plays a role in the integration of the brain network that underpins representational aspects of semantic cognition with the network that is generally associated with semantic control. In more specific terms, the proposal is that the pMTG and the IFG form part of a semantic control network that is recruited whenever the situational context requires modulation of semantic retrieval. These approaches have been more formally incorporated into the “controlled semantic cognition” (CSC) framework (Lambon Ralph et al., 2017), a two-system approach that suitably integrates the above-mentioned (and several other) ideas and findings on semantic cognition. At its core, the CSC framework assumes that a “hub-and-spoke” system (involving the ATL and modality-specific cortical areas) represents semantic knowledge, and that control over this system’s activity recruits a separate network that involves the prefrontal cortex (PFC) and the pMTG to flexibly and efficiently deploy semantically imbedded behavior. Besides the framework’s adequacy in integrating earlier findings and in generating new research questions about semantic memory processing, such as the possibility of alleviating control difficulties in SA patients (Souter et al., 2022), it is also demonstrating to be helpful in accounting for some episodic memory effects that are observable in SA patients (Cogdell-Brooke et al., 2020). In this regard, an interesting line of research has shown that SA patients have a tendency to show memory errors that can be categorized as examples of false memories (Stampacchia et al., 2018, 2019, in paired-associate recognition procedures). In terms of the CSC framework, these errors can be attributed to the patients’ difficulty in inhibiting responses that are semantically related to target items during

episodic memory tasks.

In an attempt to provide convergent evidence on the role of semantic control mechanisms in the production of false memories, in the present study transcranial direct current stimulation (tDCS) was used to modulate activity in the left posterior temporal lobe (PTL), and the behavioral effects of this stimulation were assessed adopting an experimental procedure widely utilized to induce conceptually-related false memories: The DRM task (Deese, 1959; Roediger & McDermott, 1995). A typical DRM experiment involves having participants memorize lists of words for a later test. Crucially, each list is made of words (e.g., *table, sit, legs, seat...*) that are associates of a critical lure (CL) that is a semantically related item (e.g., *chair*) but never presented at study. When they are later tested on the studied words, the participants often produce or endorse the related critical items as previously presented words. Extensive work conducted in many laboratories has documented these types of false memories under varied conditions and with different types of materials (for reviews see Gallo, 2006, 2010; Roediger & Gallo, 2022).

Memory illusions observed with the DRM procedure have been shown to always depend on the existence of some kind of relatedness (e.g., phonological, visual, or conceptual) between studied items and critical items, pointing to the central role played by the structure and dynamics of the representational systems supporting specific inter-item relations. This is most widely and clearly demonstrated in studies analyzing false recall and false recognition of unrepresented critical words following the study of meaning-related words. For example, Roediger et al. (2001) showed that a key predictor of false recall was the strength of associative connections from the study words to the critical item. The importance of the maturity and integrity of the representational network for these types of false memories has also been illustrated by experimental studies with children of different ages (Brainerd et al., 2008; Carneiro et al., 2007) and SD patients (Simons et al., 2005), as well as by brain stimulation studies aimed at modulating the neural activity in the ATL (Boggio et al., 2009; Díez et al., 2017).

Additionally, and particularly relevant in the current study, false memory production in the DRM paradigm is reliably modulated by monitoring mechanisms aimed at controlling error production at encoding and retrieval. For example, false recall and recognition are lower when conditions allow for more time at study or at test (Carneiro et al., 2012), when studied materials contain more distinctive features (Schacter et al., 2001), or when participants are given explicit warnings and instructions on how to avoid the false memories (Starns et al., 2007). Not surprisingly, efficient use of these monitoring processes is modulated by the maturity and integrity of executive control mechanisms. Thus, research has shown that specific warnings are ineffective when administered to young children (Carneiro & Fernandez, 2010), that damage in the IFG usually results in increased false recognition (Melo et al., 1999), or that cannabis consumers, who frequently display executive control impairments, exhibit higher rates of false recognition and reduced prefrontal activity than controls (Riba et al., 2015).

The DRM procedure can therefore be a very sensitive tool to test hypotheses that incorporate aspects related to both the structure of conceptual representations and the control processes operating on those representations. For this reason, in the present study, this procedure was used to investigate the potential role of the left PTL, which includes the left pMTG, in the production of false memories, using transcranial direct current stimulation (tDCS) to modulate the activity of this brain area during a DRM meaning-oriented verbal memory task. Briefly stated, tDCS involves the delivery of a low-level intensity current on the scalp through (at least) two electrodes (anode and cathode). This current is not sufficient to induce action potentials, but it allows researchers to change the response threshold of the reached neurons (Bindman et al., 1964; Brunoni et al., 2011) to investigate brain-behavior associations. The specific action mechanisms underlying the effects of tDCS in humans may depend on a number of factors that can be manipulated (i.e., electrode montage, current intensity, targeted brain area/network,

brain state prior to stimulation), which makes the technique a useful tool to better understand the neural substrates of cognition (Berryhill et al., 2014; Bestmann et al., 2015; Filmer et al., 2014). Within the logic of the present study, it was expected that tDCS of the left PTL would alter activity in the semantic control network, resulting in an increment of the rate of false recognition of conceptually-related critical lures.

The rationale to predict increased false recognition following tDCS of the left PTL is based on theoretical and empirical grounds. On one hand, the pMTG is assumed to be recruited, along with the PFC, whenever semantic control is demanded by the task at hand (Lambon Ralph et al., 2017; Wang et al., 2018), as it could be the case in detecting and rejecting CLs as part of a monitoring process in the DRM procedure. On the other hand, and as described above, previous findings suggest that impairments in executive control usually lead to enhanced false memories.

In the present study we used a standard DRM task with two types of word lists, differing in the type of semantic relatedness that linked their items with their corresponding CLs. Thus, some lists contained a set of items each with an associative relation with the list's CL (e.g., *bark, muzzle, mutt, fleas, tail, abandoned, kennel, sniff, veterinarian, and loyal*, all associated with the CL *dog*), while other lists were formed by items that were categorically related to the CL (e.g., *cat, horse, lion, tiger, elephant, cow, giraffe, pig, bull, and zebra*, categorically related to the CL *dog*). In a previous tDCS study that focused on the left ATL and utilized these same DRM tasks, Díez et al. (2017) showed that anodal stimulation at study reduced false recognition, but only for those lists formed by associates of the CLs and not for lists in which the words were categorically-related to their CL. This finding was interpreted as support for the idea that the left ATL plays a more central role as a semantic representational hub in the case of associative lists. For the present experiment, however, we expected study-phase anodal¹ tDCS of the PTL to similarly increase false recognition in both list types, since semantic control processes are likely to be required for the prevention of both associatively and categorically induced intrusions. No performance effects were expected for correct recognition as a function of the stimulation condition in any of the two list types.

2. Method

The study was not pre-registered. Adhering to open-science procedures, all the information regarding sample size determination, performance-based criteria for data exclusions, all manipulations, and all measures in the study are fully described in what follows. Stimuli, analysis scripts and raw data are available at Open Science Framework [<https://osf.io/9bkjp/>].

2.1. Participants

A total of 72 undergraduate students from the University of La Laguna, Spain, all of them native speakers of Spanish, participated voluntarily in the study, and were given course credit for their contribution. Sample size was determined to equal that used in the study by Díez et al. (2017), which proved to be adequate to reliably capture the effects of tDCS in an experiment with very similar design and procedure.

¹ Our expectation that anodal tDCS at study would modulate false recognition was based on previous findings indicating that anodal stimulation has appreciable and consistent effects on false memories in the DRM paradigm (i.e., Boggio et al., 2009; Díez et al., 2017). Specifically, these previous studies stimulating the left ATL observed behavioral outcomes (reduced false memories only after anodal tDCS) similar to those observed after applying (inhibitory) low frequency transcranial magnetic stimulation to the same brain region (Gallate et al., 2009). Still, it could be the case that cathodal tDCS could have a detrimental effect on performance when delivered over the posterior temporal lobe. For this reason, this stimulation condition was included in the study.

No participants reported suffering medical or psychological conditions that would have prevented them from receiving tDCS, including migraines, cardiac affections, brain damage, and a personal or family history of epilepsy. Only self-declared right-handed individuals were recruited to participate in the experiment, and right handedness was further assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). General information about the experiment was facilitated to participants, but no information was provided on the specific hypotheses of the experiment nor about the experimental condition that was assigned to them until each session had finished. Written informed consent to participate in the study was obtained from all participants. And the experiment, performed in compliance with the principles of the Helsinki Declaration (World Medical Association, 2013), was approved by the Ethics Committee of the University of La Laguna.

As in Díez et al. (2017), a criterion based on participants' accuracy in the recognition task was used to screen for outliers prior to conducting more specific data analyses. Specifically, a non-parametric estimate of response bias (B''_d) for each participant was calculated, and the data from participants that showed scores deviating more than 1.96 *SD* from the average response bias were discarded. This method allows for the detection of extreme response patterns and depends on measures that are not used to evaluate the main experimental hypotheses. As a result, all data from 4 participants were not included in the analyses. Thus, the final sample was composed of 68 participants (stimulation condition: anodal: $n = 22$; cathodal: $n = 23$; sham: $n = 23$). Participant's mean age was 22 years ($SD = 5.15$; range = 18–48). Eighteen participants were male and 50 were female.

2.2. tDCS protocol

We used a battery-driven tDCS stimulator (TCT Research Ltd.) to apply constant direct current at 2 mA of intensity, via rubber electrodes covered with sponges soaked with normal saline solution. Before stimulation started, and also during the stimulation period, an impedance check was performed as defined in the default mode of the tDCS device. The built-in microprocessor controller would automatically terminate stimulation if the impedance level exceeded 15 k Ω at any time. Following the protocol of previous tDCS experiments with the DRM paradigm (Alonso et al., 2021; Díez et al., 2017), the reference electrode was always placed over the right shoulder to reduce its action on the brain, and participants were randomly assigned to receive either anodal, cathodal, or sham stimulation through a 5 x 7 cm electrode over the region of interest. Critically, in the anodal experimental condition, the anode electrode was positioned on site T5 (BA37) according to the 10/20 International System of electrode placement, whereas, in the cathodal condition, it was the cathode electrode that was positioned on T5. According to a simulation with SimNIBS (4.0.1) software (Thielscher et al., 2015), this montage is likely to produce medium to high values of electrical field magnitude in the posterior temporal cortex (see Fig. 1). In the anodal and cathodal conditions, the stimulation lasted for 20 min, with 10-sec fade in and fade out ramps. Finally, in the sham condition, tDCS was applied for 1 min using the same ramps.

2.3. Design

The experimental design was mixed factorial 3(2 x 4). The between-subjects factor was stimulation type (anodal, cathodal or sham), and the within-subject factors were list type (associative or categorical) and type of word (studied, critical, distractor, or control critical). The dependent variables were the rates of hits (for correct recognition) and false alarms to critical words (for false recognition). Additional analyses were performed on measures related to signal detection theory (SDT). With the aim of further exploring the effects of stimulation on the phenomenon of false recognition, the participants' subjective recognition experience (in the form of Remember/Know judgments, as developed by Tulving, 1985) was also registered and analyzed, as described below.

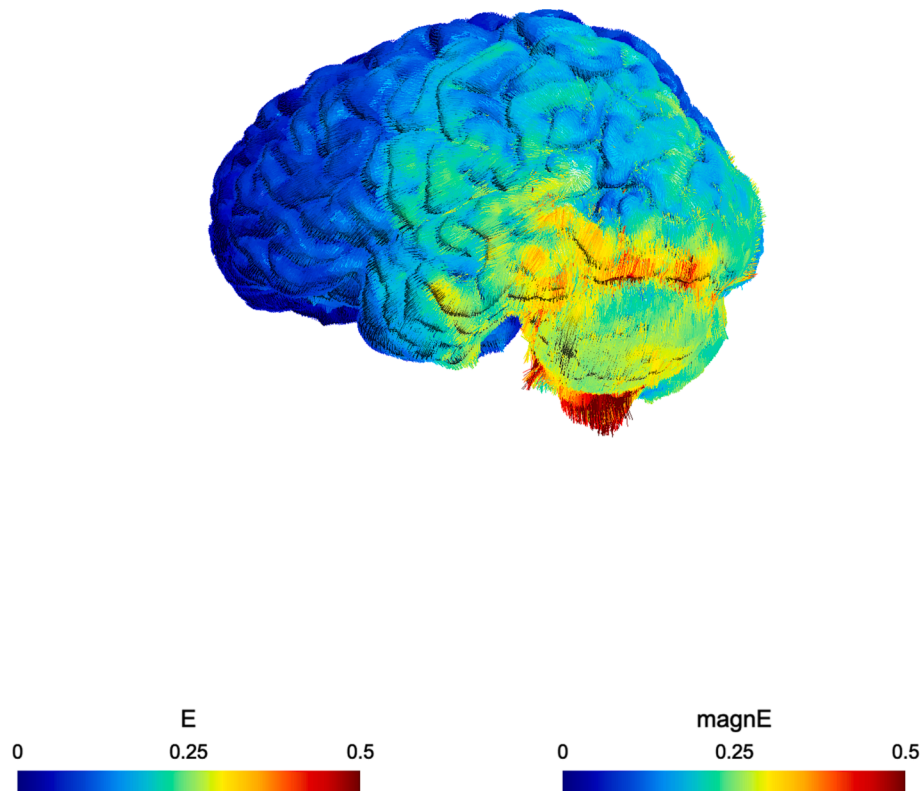


Fig. 1. SimNIBS simulation of the Maximum Average Gray Matter Normalized Electric Field produced by the tDCS montage (Anodal: T5; Cathodal: right shoulder).

2.4. Stimuli

The same stimuli sets used by Díez et al. (2017) and Alonso et al. (2021) were employed here. A total of 48-word lists were created by selecting 24 critical words that corresponded each to the most frequent item in its semantic category, in accordance with the Spanish category norms (Marful et al., 2015). Each of these critical words was then linked to a categorical list and to an associative list, acting as their respective critical lure in the memory tasks. Each of the 24 categorical lists was formed by the remaining 10 most frequently produced words in the semantic category of the critical word. An example of such a categorical list for the critical lure *car* would be: *motorbike, bus, bicycle, airplane, van, ship, tractor, motorcycle, truck, and train*. Associative lists were created by selecting the 10 strongest associates of the critical lure excluding those items that pertained to its same semantic category. To this end, backward associative strength (BAS) indices resulting from free-association norms in Spanish (Fernandez et al., 2004; Fernandez et al., 2014) were used. For instance, for the critical lure *car* the associative list was composed by the following words: *parking, motor, wheel, spin, driving, gasoline, mechanic, chauffeur, maneuver, and driver*.

2.5. Procedure

The experimental procedures were the same as in Díez et al. (2017), with the difference that the stimulation site was T5, and with the addition of remember/know judgments in the recognition test. The described procedures were the same in the three stimulation conditions, with the only difference that the stimulation ended after 1 min in the sham group. E-Prime 2.0 software (Psychology Software Tools, Inc., 2012) was used to control stimuli presentation and data recording.

Upon arrival to the laboratory, all participants completed a questionnaire designed to screen for medical or psychological conditions that could lead to their exclusion from participation in the experiment. Demographic information was also collected, and participants read and

signed an informed consent form. Then, both electrodes were placed, and the stimulation (20 min) was initiated. Because the encoding phase and an immediately following distracting task (plus the time needed for reading instructions and ensuring comprehension) lasted about 13 min, during the first 7 min of stimulation, the participants were instructed to circle the letters *n, p* and *c* in a text written in a language unknown to all participants. This visual search task served as a filler task during the idle stimulation time to minimize variability in brain/cognitive activity during stimulation. This type of stimulation (partially offline partly online) has been shown to produce larger effects than entirely offline stimulation before encoding (see Galli et al., 2019). Next, the experiment instructions were presented on a computer screen, and participants were informed that they would listen to a total of 16 lists of words, that then they would be asked to check the accuracy of several math operations, and that at the end of the experiment they would be tested on their memory for the words initially presented, without any reference to the kind of test that would be administered.

Sixteen lists of words were presented aurally to participants, with words played at intervals of 2 sec. Eight of these lists were associative and eight were categorical. The 16 lists were randomly presented to each participant, with the restriction that they were grouped in two consecutive blocks, each composed of 4 categorical lists and 4 associative lists. The presentation order for items in the categorical lists was from higher to lower categorical production frequency, and the item order in the associative lists was from higher to lower backward associative strength. Note also that list presentation was counterbalanced to ensure that all lists from the initial pool of 24 pairs of lists were presented, across participants, under all the conditions in the experimental design.

After the study phase, participants had to perform a distracting task for 2 min, in which they had to check whether displayed math operations were correct or incorrect. Finally, they had to perform a forced-choice recognition test, responding “yes” (studied earlier) or “no” (not studied earlier) to a series of probe words, with participants required to provide a Remember/Know judgment on each word identified as

studied. The instructions for this task were based on the studies by Guillery and Geraci (2010), and by Rajaram (1993), and participants read them on the computer screen. Importantly, the duration of the procedures and the stimulation time were calculated so that the stimulation ended before the beginning of the test phase. Sixty-four words were tested in the recognition task in a random order, including 32 studied words, the 16 critical words from the lists presented at study, 8 words pertaining to lists that were not presented, and the 8 critical words related to the lists that were not presented (control critical words). Words were displayed at the center of the screen, after a fixation point that lasted for 750 msec.

Upon completing the experimental session, participants filled out a questionnaire on tDCS adverse effects (Brunoni et al., 2011). None of them reported major complaints or discomfort associated with stimulation (see Table 1) Finally, participants were thanked for their contribution, and asked not to disclose information on the experiment to other students.

3. Results

Table 2 shows average recognition memory indicators for all stimulation conditions and all item types. Separate analyses for correct recognition and false recognition were performed, as reported in what follows.

3.1. Correct recognition

As shown in Fig. 2, recognition of studied words was overall high, with correct proportion ranging from 0.64 to 0.79 and few false alarms to items from unstudied lists (average = 0.06 across conditions). A 3 (stimulation condition: Anodal vs. Cathodal vs. Sham) \times 2 (type of list: Associative vs. Categorical) mixed ANOVA on hit rates ("yes" responses to studied words) revealed a statistically significant effect of type of list [$F(1,65) = 25.27$; $MS_e = 0.01$; $p < .0001$; $\eta_p^2 = 0.28$; 90 % CI [0.13, 0.41]]. On average, studied words from categorical lists ($M = 0.75$; $SEM = 0.02$) were better recognized than those from associative lists ($M = 0.65$; $SEM = 0.02$). Neither stimulation condition [$F(2,65) < 1$; $MS_e = 0.04$; $p = .77$; $\eta_p^2 = 0.008$] nor the interaction [$F(2,65) = 1.78$; $MS_e = 0.01$; $p = .18$; $\eta_p^2 = 0.05$] reached statistical significance, showing that the advantage of categorical lists over associative lists in correct recognition was not modulated by tDCS.

Nonparametric signal-detection analyses, computing A' and B'_D values, were performed to examine sensitivity and bias in the recognition responses (Donaldson, 1996; Stanislaw & Todorov, 1999). A' provides a measure of discriminability varying from 0 to 1, with a value of 0.5 indicating chance performance. B'_D provides a bias estimate, with values greater than 0 indicating conservative bias and values lower than 0 indicating liberal bias. As documented in Table 2, discriminability between studied words and distractor words was very high, ranging from 0.88 to 0.92 across materials and conditions. An ANOVA on A' showed that tDCS did not change discriminability [$F(2,65) < 1$; $MS_e = 0.01$; $p = .91$; $\eta_p^2 = 0.003$] and that there was a tendency by participants to exhibit higher sensitivity when responding to categorical lists ($M = 0.91$; $SEM = 0.01$) than to associative lists ($M = 0.88$; $SEM = 0.01$), although it did not reach statistical significance [$F(1,65) = 3.05$; $MS_e = 0.006$; $p = .09$; $\eta_p^2 = 0.04$; 90 % CI [0.00, 0.15]]. The interaction was also not significant [$F(2,65) < 1$; $MS_e = 0.01$; $p = .54$; $\eta_p^2 = 0.02$]. An examination of response bias, based on B'_D scores, revealed an overall moderate conservative tendency, with scores in the positive and ranging from 0.13 to 0.32. The corresponding ANOVA showed a significant effect of the type of list [$F(1,65) = 35.72$; $MS_e = 0.02$; $p < .0001$; $\eta_p^2 = 0.35$; 90 % CI [0.20, 0.48]], whereby participants were more conservative with associative lists ($M = 0.30$; $SEM = 0.02$) than they were with categorical lists ($M = 0.18$; $SEM = 0.03$). Neither stimulation condition [$F(2,65) < 1$; $MS_e = 0.06$; $p = .78$; $\eta_p^2 = 0.008$] nor the interaction [$F(2,65)$

$= 2.47$; $MS_e = 0.02$; $p = .09$; $\eta_p^2 = 0.07$] reached statistical significance.

Analyses were also performed on Remember/Know proportions calculated from the "yes" responses in each condition. There was an overall larger proportion of Remember responses (67 %) than of Know responses (33 %), but there were no significant effects observed for type of list, $F(1,65) < 1$; $MS_e = 0.02$; $p = .92$; $\eta_p^2 = 0.000$, stimulation condition, $F(2,65) = 1.98$, $MS_e = 0.09$; $p = .15$; $\eta_p^2 = 0.06$, or the interaction, $F(2,65) < 1$, $MS_e = 0.02$; $p = .87$; $\eta_p^2 = 0.004$.

3.2. False recognition

As shown in Fig. 3, a strong false recognition effect was observed across stimulation conditions, with a rather high recognition rate for unstudied critical words (ranging from 0.40 to 0.65 across conditions) and a moderate recognition rate for distractors that were critical words from unstudied lists (average = 0.14 across conditions). A 3 (stimulation condition: Anodal vs. Cathodal vs. Sham) \times 2 (type of list: Associative vs. Categorical) mixed ANOVA on false recognition rates ("yes" responses to critical words) showed a statistically significant effect of type of list [$F(1,65) = 5.28$; $MS_e = 0.04$; $p = .03$; $\eta_p^2 = 0.08$; 90 % CI [0.005, 0.19]]. On average, the false recognition rate was higher for categorical lists ($M = 0.54$; $SEM = 0.03$) than for associative lists ($M = 0.46$; $SEM = 0.03$). More interestingly, there was a main effect of tDCS condition [$F(2,65) = 4.24$; $MS_e = 0.08$; $p = .02$; $\eta_p^2 = 0.12$; 90 % CI [0.02, 0.23]]. Two-tailed Welch's t tests for independent samples showed that anodal tDCS ($M = 0.60$, $SEM = 0.04$) increased false recognition in comparison to sham ($M = 0.47$; $SEM = 0.04$) [$t(42.2) = 2.13$, $p = .04$, $d = 0.63$, whereas cathodal tDCS ($M = 0.44$; $SEM = 0.04$) did not differ from sham stimulation [$t(43.4) = -0.63$, $p = .53$, $d = -0.18$]. The effect of the interaction was not statistically significant [$F(2,65) < 1$; $MS_e = 0.04$; $p = .88$; $\eta_p^2 = 0.004$].

The nonparametric signal-detection analyses consisted, again, of 3 \times 2 ANOVAs on discriminability (i.e., strength of the CW) and bias estimators. The analysis on A' scores showed a significant effect for type of list [$F(1,65) = 5.04$; $MS_e = 0.03$; $p = .03$; $\eta_p^2 = 0.07$; 90 % CI [0.004, 0.19]]. Paralleling effects in correct recognition, participants exhibited higher sensitivity when incorrectly recognizing items of categorical lists ($M = 0.80$; $SEM = 0.02$) than items from the associative lists ($M = 0.76$; $SEM = 0.03$). Neither type of stimulation [$F(2,65) = 1.21$; $MS_e = 0.04$; $p = .30$; $\eta_p^2 = 0.04$] nor the interaction [$F(2,65) < 1$; $MS_e = 0.03$; $p = .94$; $\eta_p^2 = 0.002$] reached statistical significance. Bias scores (B'_D) evidenced, as it was the case in correct recognition, an overall tendency towards conservative responding, with scores ranging from 0.18 to 0.48. Although there was, as in the case of correct recognition, a tendency for more conservative responses in the case of associative lists than in the case of categorical lists (averages of 0.40 vs 0.32), the ANOVA showed that the difference only approached statistical significance [$F(1,65) = 3.72$; $MS_e = 0.06$; $p = .06$; $\eta_p^2 = 0.05$; 90 % CI [0, 0.16]]. Stimulation condition had a significant effect on response bias [$F(2,65) = 3.47$; $MS_e = 0.17$; $p = .04$; $\eta_p^2 = 0.10$; 90 % CI [0.003, 0.20]]. Two-tailed Welch's t tests showed that while cathodal tDCS ($M = 0.45$; $SEM = 0.05$) and sham stimulation ($M = 0.40$; $SEM = 0.06$) did not significantly differ from one another [$t(42.5) = 0.53$; $p = .60$; $d = 0.16$], responding was more liberal after anodal tDCS ($M = 0.23$; $SEM = 0.07$) than after sham stimulation [$t(42.8) = -1.88$; $p = .07$; $d = -0.56$], but this effect was only marginally significant. The interaction was not significant [$F(2,65) < 1$; $MS_e = 0.06$; $p = .87$; $\eta_p^2 = 0.004$].

Finally, the overall rates of Remember (47 %) and Know (53 %) responses were similar, and the ANOVA revealed a main effect of type of list, $F(1,65) = 6.67$; $MS_e = 0.06$; $p = .01$; $\eta_p^2 = 0.09$; 90 % CI [0.012, 0.213], so that the proportion of Know responses was higher in categorical ($M = 0.59$; $SD = 0.33$) than in associative lists ($M = 0.47$; $SD = 0.30$). Neither stimulation condition, $F(2,65) < 1$; $MS_e = 0.13$; $p = .17$; $\eta_p^2 = 0.05$, nor the interaction reached statistical significance, $F(2,65) < 1$; $MS_e = 0.06$; $p = .17$; $\eta_p^2 = 0.003$.

Table 1

Descriptive statistics (mean and standard deviations) of the participants' responses to the questionnaire on tDCS adverse effects. Side-effects were rated on a scale ranging from 1 to 4 (1: absent; 2: mild; 3: moderate; 4: severe).

	Anodal	Cathodal	Sham	χ^2	*p	Pairwise comparisons
Headache	1.27 (0.46)	1.35 (0.49)	1.35 (0.65)	0.32	0.853	
Neck Pain	1.18 (0.39)	1.09 (0.29)	1.09 (0.29)	1.27	0.530	
Scalp pain	1.18 (0.39)	1.09 (0.42)	1.13 (0.42)	2.09	0.352	
Tingling	2.36 (0.90)	1.96 (0.64)	1.87 (0.75)	4.40	0.111	
Stinging/itching	2.18 (0.80)	1.57 (0.73)	1.61 (0.84)	9.38	0.009	A > C; A > S
Burning sensation	1.23 (0.53)	1.26 (0.62)	1.26 (0.54)	0.104	0.949	
Reddening of the skin	1.77 (0.97)	1.52 (0.67)	1.04 (0.21)	11.657	< 0.003	A > S; C > S
Drowsiness	1.41 (0.73)	1.17 (0.39)	1.52 (0.73)	3.036	0.219	
Concentration problems	1.77 (0.53)	1.35 (0.49)	1.74 (0.63)	7.149	0.028	A > C
Severe mood swings	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	0.00	1.00	

* p values from Kruskal-Wallis tests.

Table 2

Mean recognition results and standard error as a function of type of list and type of stimulation.

	Associative			Categorical		
	Anodal	Cathodal	Sham	Anodal	Cathodal	Sham
<i>Studied Words</i>						
Correct Recognition	0.64 (0.04)	0.65 (0.04)	0.65 (0.03)	0.79 (0.02)	0.73 (0.04)	0.73 (0.04)
Sensitivity (A')	0.88 (0.02)	0.88 (0.02)	0.89 (0.01)	0.92 (0.01)	0.91 (0.01)	0.89 (0.02)
Bias (B' _p)	0.32 (0.04)	0.29 (0.04)	0.30 (0.03)	0.13 (0.04)	0.22 (0.05)	0.19 (0.05)
Remember	0.71 (0.05)	0.60 (0.06)	0.69 (0.05)	0.70 (0.04)	0.59 (0.05)	0.71 (0.05)
Know	0.29 (0.05)	0.40 (0.06)	0.31 (0.05)	0.30 (0.04)	0.41 (0.05)	0.29 (0.05)
<i>Critical Words</i>						
False recognition	0.55 (0.05)	0.40 (0.05)	0.44 (0.06)	0.65 (0.05)	0.47 (0.04)	0.51 (0.05)
Sensitivity (A')	0.78 (0.04)	0.71 (0.05)	0.71 (0.05)	0.83 (0.02)	0.79 (0.03)	0.78 (0.04)
Bias (B' _p)	0.28 (0.08)	0.48 (0.06)	0.43 (0.07)	0.18 (0.07)	0.41 (0.07)	0.38 (0.07)
Remember	0.61 (0.06)	0.45 (0.07)	0.53 (0.07)	0.47 (0.06)	0.34 (0.07)	0.44 (0.08)
Know	0.39 (0.05)	0.55 (0.07)	0.47 (0.07)	0.53 (0.06)	0.66 (0.07)	0.56 (0.08)
<i>Distractors</i>						
Unstudied list items	0.05 (0.02)	0.05 (0.02)	0.04 (0.02)	0.08 (0.03)	0.05 (0.02)	0.09 (0.03)
Unstudied critical items	0.17 (0.05)	0.12 (0.03)	0.13 (0.04)	0.17 (0.04)	0.12 (0.04)	0.12 (0.04)

4. Discussion

In view of recent empirical evidence and theoretical developments that propose that the left pMTG is a relevant component in a semantic control network (Lambon Ralph et al., 2017), the experiment reported here used tDCS over the left PTL to alter semantic control while participants performed an episodic memory task. Specifically, we used an experimental procedure, known as DRM, that has proven to be useful in inducing conceptually-based false recognition that is contingent on both activation and control processes. To the extent that semantic control is reliant on the pMTG to restrain false memories, it was expected that altering neural activity in this region should specifically affect the rate of false alarms to (unstudied) critical items, regardless of the kind of semantic relatedness between studied items and those critical items.

In line with earlier empirical evidence (Alonso et al., 2021; Boggio et al., 2009; Díez et al., 2017; Gallate et al., 2009), tDCS during the study phase of the experiment did not alter the pattern of recognition responses to studied words. Neither hits, nor sensitivity, nor response bias were modulated by the stimulation. The usual advantage of categorical lists over associative lists in correct recognition, independently of

stimulation conditions, was also observed (Alonso et al., 2021; Díez et al., 2017). Likewise, the habitual higher proportion of Remember over Know responses assigned to studied items was not affected by stimulation.²

The pattern of results in the case of false recognition was, however, substantially different as a function of stimulation conditions. Anodal tDCS over the left PTL increased false recognition in comparison to sham stimulation for both types of DRM lists. Hence, regardless of the nature of the relatedness, associative or categorical, between critical items and studied words, anodal tDCS rendered participants more prone to false recognition. As further discussed below, this finding fits well with the idea that the left pMTG is a key component of the semantic control network, with a role in constraining retrieval by reducing the influence of contextually-inappropriate semantically-related information (Krieger-Redwood & Jefferies, 2014).

The behavioral outcome of the stimulation in the present study, together with the differential patterns of false recognition effects observed in related studies (Alonso et al., 2021; Díez et al., 2017), is suggestive of highly specific tDCS effects when delivered over distinct brain regions configuring the semantic network. Moreover, the entirely

² As noted, Remember and Know responses tied to the false recognition of critical words were also unaffected by stimulation in any significant way. Because of the admittedly exploratory nature of the question, and in view of the null effects of the manipulation, the issue of how tDCS could modulate the subjective experience accompanying recognition responses is not further discussed here.

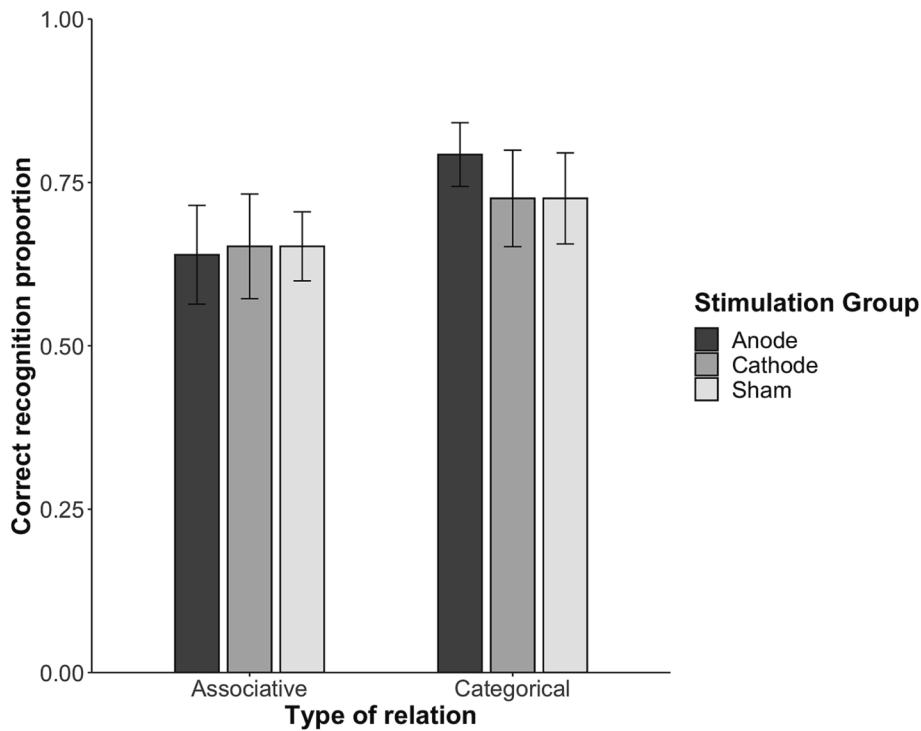


Fig. 2. Correct recognition proportion as a function of Stimulation and List Type. Error bars represent 95% confidence intervals (CI).

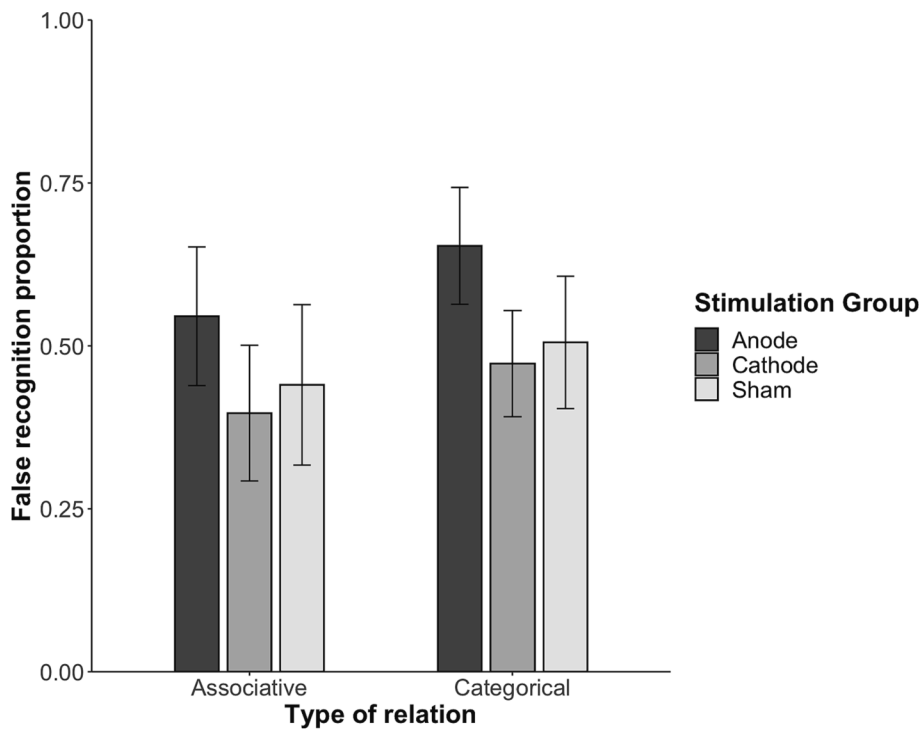


Fig. 3. False recognition proportion as a function of stimulation and type of list. Error bars represent 95% confidence intervals (CI).

different pattern of false recognition modulation observed in [Díez et al., \(2017\)](#): reduced false recognition only in associative lists) and the present study (enhanced false recognition in both kind of lists) entails a behavioral dissociation that fits well into the CSC framework ([Lambon Ralph et al., 2017](#)), with its representational “hub-and-spoke” system (involving the ATL and modality-specific cortical areas) and its separate semantic control network (that includes the inferior lateral PFC and the

pMTG).

Our finding of enhanced production of false recognition following stimulation of the left PTL is compatible with the idea that this region is directly involved in semantic control. Results from a number of studies with the DRM paradigm indicate that detecting and rejecting critical lures recruit monitoring processes that may significantly reduce the production of false memories (e.g., [Carneiro et al., 2012](#); [Melo et al.,](#)

1999; Schacter et al., 2001), with the efficiency of these processes relying on the integrity of control mechanisms. Thus, patients with structural and/or functional damage in the left perisylvian area (most likely affecting the pMTG) have been shown to exhibit intact true recognition but enhanced false recognition of semantically-related foils (Jefferies & Lambon Ralph, 2006; Rogalski et al., 2007), which parallels our main finding here. Since semantic control has been proposed to recruit a (rather left-lateralized) brain network that includes the PFC and the pMTG (Davey et al., 2016; Lambon Ralph et al., 2017; Thompson et al., 2022), a reasonable possibility is that applying anodal tDCS over the PTL altered functional connectivity within this network rendering participants specifically vulnerable to semantic intrusions (it should be noted that anodal stimulation did not lead participants to produce more false alarms to control unrelated critical words; see further discussion below). Although the left PTL has not been a target in studies on false memory (either using neuroimaging or neuro-modulation techniques), a few tDCS studies have already focused on posterior temporal areas to explore the effects of stimulation on language-related functions (i.e., Henseler et al., 2014), given the widely accepted implication of these regions in language production and comprehension (Friederici, 2012). Interestingly, the main result of one of these studies seems to align with the idea that anodal tDCS over the left posterior temporal gyrus (pMTG/STG) affects semantic control-related neural activity (Pisoni et al., 2012), showing that stimulating this region selectively induced slower reaction times when naming pictures presented in semantically-homogeneous blocks (likely to generate semantic interference) but not when the blocks were semantically unrelated.

While our main finding is consistent with the role of the pMTG in semantic control, we recognize that the relatively low spatial resolution of tDCS makes other interpretations possible, which is a limitation to be considered for future studies. In our montage, the critical electrode was positioned on the left PTL, specifically on site T5 (BA37), which ensures stimulation of the left pMTG but also encompasses the left posterior inferior temporal gyrus and nearby occipitotemporal areas. It is unclear how neuromodulation of these surrounding areas might have reduced the participants' ability to say no to critical words. The lateral temporal cortex is thought to be a semantically relevant region within the default mode network (i.e., Humphreys et al., 2015) that might maintain relevant information to bias ongoing processing (Crittenden et al., 2015; Smith et al., 2018). Moreover, activation in posterior temporal regions has been associated with engagement in more difficult conditions of a variety of tasks (Fedorenko et al., 2013) that can be hard to disentangle from the implication of control mechanisms. Additionally, we cannot entirely discard the possibility that our monopolar temporal montage could make the posterior parietal cortex (PPC) a receptor of the stimulation, even when this kind of montage is thought to improve focality (Woods et al., 2016). It is well recognized that the PPC is a core region within the fronto-parietal network (Nee, 2021), a general-domain cognitive control network which is spatially distinct from the semantic control cortex of pMTG (Jackson, 2021), and that is also involved in memory retrieval (Sestieri et al., 2017). Hence, neuromodulation of this area could potentially impact on retrieval tasks demanding control. Pergolizzi and Chua (2015, Exp. 2), for example, used a DRM paradigm and applied anodal tDCS over the left PPC (with the cathode over the right PPC) for 20 min during retrieval. Relative to sham, this specific bilateral montage left true recognition intact but led to an increase of false recognition. Importantly, this effect of tDCS was not limited to critical lures (semantically related to targets) and also affected semantically unrelated lures, a pattern of results that largely differs from the one observed in the present study and is compatible with the notion that tDCS over the PPC interfered with neural activity that was not specifically associated with semantic control. Hence, while we cannot rule out a PPC modulation in our study, our results would seem to speak in favor of tDCS-induced interference over semantic control. The inclusion in future studies, as a control site, of an experimental condition in which

the PPC is stimulated would be of special relevance to better understand the specific role of the PTL in semantic control.

The specific neural mechanisms underlying our main finding of increased false recognition following study-phase stimulation of the left PTL remain to be fully understood. As suggested above, our main result fits well with a disruptive (inhibitory) behavioral effect of anodal tDCS over the left PTL (thought to be involved in semantic control) by altering PFC-PTL connectivity, which aligns with the effect observed in previous studies in which anodal stimulation of the ATL (thought to be involved in the production of false memories) reduced false recognition. While anodal tDCS is frequently (and erroneously) seen as facilitatory stimulation, it is important to bear in mind that the aftereffects of tDCS in cognitive domains are not always polarity-specific (Jacobson et al., 2012; see also Fertonani & Miniussi, 2017) and that anodal tDCS can lead to performance that is compatible with altered brain functioning (i.e., Díez et al., 2017; Gómez-Ariza et al., 2017; King et al., 2020; Mondino et al., 2016). In this regard, it would be valuable that future tDCS studies aimed at more specifically determining the role of the pMTG in semantic control include brain activity recordings, as tDCS has been shown to elicit brain changes at different levels (from sub-cellular to network functioning) depending on a number of factors (e.g., previous state, current intensity, stimulation duration, electrode montage, polarity, or target site) (see Das et al., 2016; McDermott et al., 2019). For example, tDCS has been shown to change local synchronization and connectivity patterns by modulating specific frequency bands (i.e., Mancini et al., 2016) and to change neurotransmitter concentrations (Kim et al., 2014; Stagg et al., 2009), and these neural effects could potentially contribute to the behavioral effects observed in the present study. Also, further research including designs that incorporate features such as control tasks and control stimulation sites, plus the combined use of non-invasive stimulation with neuroimaging techniques could greatly contribute to clarify the function of the posterior temporal region in semantic processing.

In the meantime, and in spite of the acknowledged limitations, the present results provide preliminary causal evidence consistent with the idea of a semantic control network that includes the pMTG as a key component and, more broadly, with a theoretical framework in which semantic cognition depends on the interaction between control and representational systems.

CRediT authorship contribution statement

María A. Alonso: Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Emiliano Díez:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Antonio M. Díez-Álamo:** Writing – review & editing, Methodology, Conceptualization. **Angel Fernandez:** Writing – original draft, Methodology, Conceptualization. **Carlos J. Gómez-Ariza:** Writing – original draft, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Stimuli, analysis scripts and raw data are available at Open Science Framework [<https://osf.io/9bkjp/>].

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