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Citation for final published version:

Jones, Scott P., Wigmore, Lewys, Ajayi, Bailey, Reid, Harriet and Dwyer, Dominic M. 2025. Static outcomes: Anodal tDCS at Fp3, or P3, does not modulate perceptual learning as indexed by the intermixed-blocked effect. *Journal of Experimental Psychology: Animal Learning and Cognition*

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Static outcomes: Anodal tDCS at Fp3, or P3, does not modulate perceptual learning as indexed by the intermixed-blocked effect.

Scott P. Jones¹, Lewys Wigmore¹, Bailey Ajayi¹, Harriet Reid¹, and Dominic M. Dwyer²

¹Psychological Sciences Research Group, University of the West of England, Bristol, United Kingdom,

²School of Psychology, Cardiff University, Cardiff, United Kingdom.

Running head: ANODAL tDCS FAILS TO MODULATE *IBE*

Brief Communication

September 2025 – Revision in preparation for:

Journal of Experimental Psychology:

Animal Learning and Cognition

Address for correspondence:

Dr Scott. P. Jones

School of Social Sciences

University of the West of England

Coldharbour Lane

Bristol

BS16 1QY

E-mail: scott6.jones@uwe.ac.uk

Abstract

Perceptual learning can be defined as a relatively permanent change in discrimination performance as a result of experience or exposure. One key index of perceptual learning is the intermixed blocked effect (*IBE*) in which exposure to two ambiguous or perceptually similar stimuli (i.e., AX & BX) exposed in an intermixed fashion (AX, BX, AX, BX, AX, BX) produces enhanced discrimination performance compared with blocked exposure (AX, AX, AX, BX, BX, BX). Previous imaging data has implicated multiple brain regions in the *IBE*. In the present study, Transcranial Direct Current Stimulation (tDCS) was used to explore the causal relationship of two regions, the dorsolateral prefrontal cortex (DLPFC) and posterior parietal cortex (PPC), to performance. A mixed, double-blind, design administered two online sessions of tDCS (active and sham) to 48 participants, while they viewed pairs of similar stimuli. Half of the participants received active stimulation to the DLPFC, and the other half to the PPC. Anodal stimulation in either the DLPFC or the PPC provided no modulation of discrimination performance relative to sham stimulation. These results potentially question the generality of the interpretation of other studies in which stimulation of these areas does impact on other indices of perceptual learning.

Keywords: Brain Stimulation, Visual Perception, Learning, Exposure Schedules

Perceptual learning refers to the relatively permanent improvement in the ability to discriminate between similar stimuli as a result of experience. Gibson (1963, p. 29) defined this type of learning as “any relatively permanent and consistent change in the perception of a stimulus array, following practice with this array”. The changes that occur as a result of such exposure have been extensively studied across a range of species and modalities (for reviews see, Goldstone, 1998; Mitchell & Hall, 2014). Across many experimental demonstrations of perceptual learning stimuli are often described in abstract terms (i.e., AX, BX etc...) and classified based on their common (X) and unique (A or B) features.

One theory used to explain perceptual learning is the model proposed by McLaren, Kaye & Mackintosh, (1989). Known as the MKM model, this theory posits that perceptual learning is a multifaceted process that involves the selective reduction in salience for common features, the formation of more stable and accurate representations of internal representations of complex stimuli (unitization), and the development of inhibitory associations between unique elements. All of which potentially contribute to improved discrimination and reduced generalization. Thus, the model explains perceptual learning via multiple mechanisms (see, McLaren & Mackintosh 2000, McLaren, Forrest & Mackintosh, 2012). Several recent studies, which have demonstrated a disruption of perceptual learning due to anodal tDCS stimulation are been cited as supporting aspects of this model of learning (Civile, Cooke, et al., 2020; Civile & McLaren, 2022; Civile, McLaren, et al., 2020, 2021; Civile, McLaren, & McLaren, 2018; Civile, Quaglia, et al., 2021; Civile, Waguri, et al., 2020).

This line of research has focused on the effect of anodal tDCS to the left dorsolateral prefrontal cortex (DLPFC), which has been shown to disrupt perceptual learning effects as

indexed by face and checkerboard inversion effects – namely the higher accuracy in memory for upright over inverted exemplars (see, Civile et al., 2016). In this context, inversion effects are seen as a proxy for perceptual learning due to previous studies that have found that artificial prototype-defined checkerboards demonstrate the typical inversion effect following familiarization (Civile, Zhao, et al., 2014; McLaren & Civile, 2011), which are then attenuated by DLPFC anodal stimulation. The MKM model explains this inversion effect, for both faces and checkerboards, as the result of salience modulation. According to the model, features that are reliably predicted by other co-occurring features accrue low prediction error and, consequently, undergo a reduction in salience or activation. In contrast, novel or less predictable features maintain or even increase their salience. When applied to prototype-defined categories, the model predicts that features common to exemplars—those defining the prototype—gradually lose salience with repeated exposure, thereby reducing generalization among exemplars. As a result, unique features become more salient by comparison, facilitating discrimination. In categorization tasks, this mechanism implies that frequently presented common features, being highly predictable, lose salience quickly and are slower to form new associations, further shaping task performance.

In this light, a plethora of studies have found that anodal stimulation to the DLPFC impairs inversion effects with familiar stimuli and thus may impair this salience modulation (Civile, Cooke, et al., 2020; Civile & McLaren, 2022; Civile, McLaren et al., 2021; Civile, Quaglia, et al., 2021; Civile, Waguri, et al., 2020). Here, the effect of anodal stimulation has been explained in terms of prior preexposure to a prototype-defined category no longer enhancing the discriminability of exemplars from that category. Instead, it may increase generalization among them. Shared (common) features across exemplars become more salient due to mutual coactivation, whereas unique features—those present in only one or a few exemplars—remain less salient. This alteration in perceptual learning is thought to

underlie the observed reduction in the inversion effect, as it diminishes participants' ability to discriminate among upright faces, effectively making them appear more similar to one another and thus reducing or removing the usual advantage for upright over inverted stimuli. This disruption has been found across many variations of inversion tasks.

Importantly, the inversion effect is not the most common measure of perceptual learning (see, Mitchell & Hall 2014; Hall 2017; and Hall 2021 for reviews). Thus, to test the generality of the previous findings it is important to consider whether anodal stimulation can disrupt other notable indices of perceptual learning. One such index is the intermixed-blocked effect (e.g., Honey, Bateson & Horn, 1994; Mundy, Honey & Dwyer, 2007; Symonds & Hall, 1995). When total exposure is matched, intermixed exposure (i.e., AX, BX, AX, BX...) typically produces better discrimination than blocked presentation (i.e., AX, AX..., BX, BX...) (e.g., Honey, Bateson & Horn, 1994; Mundy, Honey & Dwyer, 2007; Symonds & Hall, 1995). This finding is key in establishing that perceptual learning is not simply about the amount of exposure, and has been highly influential in driving theory development (e.g., Artigas & Prados, 2014; Dwyer, Mundy & Honey, 2011; Hall 2003; Mundy et al., 2006; McLaren and Mackintosh, 2000; Mitchell, Nash, & Hall, 2008), which makes applying stimulation while performing a task that elicits the intermixed blocked effect (*IBE*) a useful test case for assessing the generality of tDCS stimulation effects. Moreover, examining DLPFC effects using anodal stimulation and the *IBE* might help elucidate some of the mechanisms of the *IBE*. One of the proposed mechanisms for the *IBE* from MKM is salience modulation (McLaren, Kaye & Mackintosh, 1989, McLaren & Mackintosh, 2000) – with the prediction that this will enhance the salience of stimulus unique elements over elements common across stimuli. Thus, if salience modulation is disrupted through anodal stimulation of the DLPFC, as suggested by previous studies on inversion (Civile, Cooke, et al., 2020; Civile et al., 2019; Civile & McLaren, 2022; Civile, McLaren et al., 2021; Civile, Quaglia, et

al., 2021; Civile, Waguri, et al., 2020), then the *IBE* should also be disrupted to the extent it also relies on salience modulation. In addition, studies of tDCS anodal stimulation of the posterior parietal cortex (PPC) have been shown to influence perceptual tasks (Clark et al., 2012; Filmer, Dux & Mattingley, 2015; Hiraga et al 2025). For example, Hiraga et al., (2025) have found that anodal stimulation during a grating discrimination task enhanced performance relative to sham. Thus, examining PPC stimulation will assess whether these previous effects generalize to impacting on the *IBE*.

Importantly, there is already some evidence for both DLPFC and PPC involvement in the *IBE* and other perceptual learning effects from fMRI studies (see, Dwyer & Mundy 2015 for a review). In particular, Mundy and colleagues (2009, 2013, 2014) have shown that differences in perceptual learning based on exposure schedules are associated with changes in activity within the visual cortex and frontoparietal regions. In their study participants were exposed to confusable pairs of faces, scenes and dot patterns in an intermixed or blocked fashion before a same/different discrimination task asked them to make discrimination judgements about either exposed or novel pairs. It was found that frontal and parietal cortical areas, including the intraparietal sulcus (IPS - a structure within the PPC), frontal and supplementary eye fields and dorsolateral prefrontal cortex were activated during the task and related to performance. In particular, the DLPFC and the PPC (specifically, IPS) were the key frontoparietal regions involved in non-stimulus specific discrimination improvements. Related patterns of brain activation have also been observed in attentional control areas such as the superior frontal gyrus, mid-frontal gyrus, and cingulate gyrus—regions previously implicated in perceptual learning by Mukai et al. (2007).

It should also be noted that the fMRI data suggests that many other areas are implicated in the *IBE*, and perceptual learning more generally. In the same set of studies, Mundy et al. (2009, 2014) demonstrated stimulus independent activation within the visual

cortex, and that the pattern of activity changed based on the nature of exposure. Importantly, this correlated with performance, similar to the frontal parietal areas, indicating that demands on these areas decreased as discrimination performance improved. More generally, similar patterns of activation have been shown during visual discrimination tasks (e.g., Schiltz et al., 1999; Dubois et al., 1999; Mukai et al., 2007; cf. Schwartz et al., 2002). Taken together, these findings suggest that perceptual learning involves both bottom-up (visual and parietal cortex) and top-down (frontoparietal) processes (for an extended discussion of this issue see Dwyer & Mundy, 2015; Mitchell and Hall, 2014).

However, fMRI evidence is intrinsically correlational, and thus, tDCS presents an important and novel method for furthering causal understanding of the mechanisms that underpin the *IBE*. In particular, via the prediction that salience modulation can be disrupted by anodal stimulation, which in turn should disrupt the *IBE* to the extent it relies on this mechanism. Imaging studies have suggested multiple regions involved in these learning effects and anodal stimulation, namely of the DLPFC and PPC have been shown to disrupt other forms of perceptual learning. In the current study, anodal tDCS is applied to the DLPFC and PPC while manipulating exposure schedules to investigate whether this disrupts the *IBE*. If effects of stimulation are observed, this will provide evidence that DLPFC and PPC regions play a causal role in modulating perceptual learning, strengthen the evidence for the account provided by the MKM model, and thus potentially provide additional evidence for the theoretical mechanisms which underpin perceptual learning. In contrast, a clear null effect of anodal tDCS stimulation on the *IBE* would potentially question the generality of DLPFC or PPC involvement across different perceptual learning procedures and effects.

Method

Participants

An a-priori Bayesian power analysis using the BFDA package for Bayesian design analysis was used to obtain a sample size (Schönbrodt & Wagenmakers, 2018). Assuming a large effect size (Cohen's $d = 0.8$), derived from previous literature on the interaction between perceptual learning task and type of stimulation (e.g., Exp 1a, Civile et al., 2021). Setting a boundary of $BF_{10} > 6$ for the difference between the stimulation conditions (i.e., a within-subjects comparison of Anodal vs Sham), the simulation reached 89.8% conclusive results at the H1 boundary and 10.2% inconclusive results, suggesting that an N of 24 is a feasible stopping point. To align with the design of the study and the counterbalance, the final sample consisted of a total of 48 psychology undergraduates (27 females, 21 males), 24 participants per stimulation site between the ages of 19 and 64 years ($M = 23.20$, $SD = 8.66$) who were recruited from the University of the West of England. Participants received course credit as compensation. All participants were naïve to stimulation, right-handed, had normal or corrected-to-normal vision, and no history of neurological, psychiatric, or mental illness.

Stimuli

The experiment used 18 pairs of each type of stimuli (i.e., faces, scenes, checkerboards, and dot patterns) drawn from previous perceptual learning studies examining the intermixed blocked effect (Mundy et al., 2007, 2009, 2014; Jones et al., 2023). Figure 1 displays examples of these stimuli as well as examples of trial sequences. The method of stimulus creation is outlined in detail in previous fMRI studies on the intermixed blocked effect (i.e., Mundy et al., 2009; 2014). Briefly, dot and checkerboard patterns were created using a custom visual basic script. For dot patterns, 11 black dots filled a white background with a second pattern adjusted the location of four dots randomly to create the corresponding pair.

For checkerboards three elemental patterns were created A, B & X and these were overlaid to create each checkerboard pair. For face stimuli nine male and nine female faces were created by selecting end points of two same sex faces and morphing along a continuum using Morpheus 1.85 (ACD Systems, Saanichiton, British Columbia, Canada). Scene stimulus pairs were computer generated virtual rooms, created using a computer games editor (Deus Ex, Ion Storm L.P, Austin, TX, USA) and software editor (Deus Ex, Software Development Kit). Stimuli were presented through a HP PC with a 24" HP monitor (1920 x 1080 pixels; 60Hz) via PsychoPy (Version 2024.2.5). All stimuli were presented in the centre of the screen and measured 300 x 300 pixels. The images were surrounded by a grey background and viewed at a distance of 60cm, with an approximate visual angle of $7.6^\circ \times 7.6^\circ$ for each image.

Design & Procedure

Each participant completed two sessions in a within-subject design. Each session comprised a perceptual learning task during which participants received exposure to pairs of similar stimuli before completing a discrimination task that assessed learning. There were two sessions per participant, one with anodal tDCS and the other with sham stimulation (see section below for details of stimulation). Stimulation (i.e., anodal or sham) was delivered during each exposure phase and was triggered by the onset and offset of the first and last stimulus presentation. During exposure, participants passively viewed pairs of similar stimuli from a set of four different stimulus classes, i.e., dots, checkerboards, faces and scenes. Within each exposure, half the stimuli were exposed in an intermixed fashion (e.g., AX, BX, AX, BX, etc...) and the other half exposed in a blocked fashion (e.g., CY, CY..., DY, DY...). Stimuli were presented sequentially for 2 s with only one of the pair appearing on screen at any given time with a 400ms inter-stimulus-interval (ISI) between presentations. In each session there were eight blocks of exposure, two per stimulus class, followed by a

discrimination test (see Figure 1 Panel A for a schematic example of an exposure trial). After each exposure block, participants were asked to complete a same-different discrimination task during which they made judgements on stimuli pairs that were either displayed during exposure (i.e., intermixed and blocked), or were novel to give a baseline measure of performance without perceptual learning. Participants were presented with each stimulus from a pair one at a time. On ‘same’ test trials (see Figure 1 Panel B for example) there were two presentations of the same stimulus (e.g., AX/AX or BX/BX). On ‘different’ test trials, both stimuli from a pair were presented, with the identity of the first stimulus counterbalanced such that each occurred first and second equally often (e.g., AX/BX or BX/AX). On each trial, the first stimulus was presented for 500ms, followed by a random mask screen for 300ms, then the second stimulus for 500ms. Participants were instructed to press “Z” to respond “same” and “M” for “different”. This instruction remained on screen until a response had been made. A response limit of 2000ms was enforced following the offset of the second stimulus presentation. The discrimination phase ran in four blocks, and in each block participants are given 12 trials (comprising four intermixed, four blocked, and four novel trials), presented in a random order. Half of the trials comprised the same stimuli and the other half presented two different stimuli from a pair. After each block, participants were allowed to take a short break and continue by pressing the spacebar. After each discrimination, the next exposure phase began.

Participants were given a minimum of 48 hours between sessions. Following each session, participants were asked to rate their subjective experience of discomfort, heat, fatigue, and pain using a scale from 1-5, alongside any adverse effects that they had experienced in the 24 hours post stimulation. Using the same 1-5 Likert type scale, participants were asked to indicate the extent to which they felt their performance on the task was influenced by their perceived sensations.

The experiment was counterbalanced such that within each experimental session four exposure phases began with intermixed exposure followed by blocked exposure and four began with blocked followed by intermixed. The order of which was randomized for each participant. The assignment of stimuli to conditions (i.e., blocked, intermixed, and novel) and the order of stimulation (anodal and sham) was counterbalanced across participants such that different versions of the task rotated pairs of stimuli through assignment to blocked, intermixed, and novel conditions. The assignment of anodal or sham stimulation session was split equally such that half the participants received sham stimulation followed by anodal and the other half received anodal first and then sham stimulation. The assignment to condition was randomized across participants.

tDCS apparatus and montage

Transcranial stimulation was delivered through a NuroStym tES battery-driven stimulator (NeuroDevice, BrainBox) using two 5×5 cm rubber electrodes encased in saline-soaked sponges. In the anodal (i.e., active) condition, a direct current of 2mA was delivered. Electrodes were positioned, according to the 10-20 EEG system, at locations for DLPFC (i.e., F3, reference at Fp2) stimulation and PPC (i.e., P3, reference at T4) stimulation. Cathodal stimulation is defined relative to the reference electrode in both cases. A computational current flow model was computed a-priori using the SimNIBS package (Thielscher, Antunes & Saturnino, 2015). This simulation confirms two distinct cortical electrical fields were produced by the two different montages (see, figure 2). The current and electrode size equates to a current density of 0.08. Stimulation ramp-up and fade-out occurred during the first and last 7 s of each exposure period. In the anodal condition, the stimulation continued through the exposure periods, while in the sham condition current was delivered during two ramp-up and ramp down epochs at the beginning and the end of stimulation (see figure 1), consistent

with previous demonstrations of sham stimulation (for review see, Fonteneau et al., 2019). A double-blind procedure was employed such that a third-party programmed the stimulation settings on the device. An experimenter, who was unaware of the type of stimulation, administered the montage using codes provided by the third party. Stimulation was delivered in an online fashion meaning that the current was delivered during part of the task. Stimulation lasted for the duration of the exposure phase. This resulted in a total duration of 8 minutes of stimulation across the 8 blocks of exposure. It is worth noting that stimulation protocols of <10mins at 2mA have been shown to produce effects at the DLPFC on other tasks (see, Tremblay et al., 2014). For stimulation at the PPC there are studies that have stimulated at 2mA (e.g., Hirayama et al., 2021), but few examples of stimulation of <10mins. That said, there is evidence that stimulation of >1min to the PPC produces various changes in activity as measured through EEG signals (Mangia, Prini & Cappello, 2014).

Data treatment

In the present study, both null hypothesis significance testing (NHST) and Bayesian inference were employed to evaluate our experimental results. NHST was used to determine whether observed effects reached conventional thresholds for statistical significance (e.g., $p < .05$), providing continuity with widely accepted practices in psychological research.

Complementing this approach, Bayesian analyses was applied to quantify the relative evidence for the null and alternative hypotheses using Bayes factors. This allowed us not only to detect statistically significant effects, but also to assess the degree of support for the absence of an effect—something NHST cannot directly provide. For the frequentist analysis, main effects and interactions from a factorial ANOVA with the within-subjects factors of exposure (intermixed, blocked, and novel), trial type (same or different), and stimulation type (anodal & sham), alongside the between-subjects factor of montage (DLPFC, PPC) are

presented with the alpha level set at .050. Effect sizes are reported as partial eta squared (η^2).

A Bayesian statistical approach was used to quantify evidence for or against the null by computing Bayes Factors (BFs). The analysis was conducted using Jamovi (Jamovi Team, 2024) with the BayesFactor R package (Morey & Rouder, 2023) using default prior settings for model comparisons and post hoc tests were used. A Cauchy prior distribution centered on 0 with a scale of $r = \sqrt{2}/2$ was used for all default t-tests. Posterior model probabilities and Bayes factors were computed using the Bayes Factor module, and corrections for multiple comparisons were applied using the method proposed by Westfall, Johnson, and Utts (1997). BF_{excl} values quantifies how much more likely the data are with the effect excluded compared with models where it is included are reported. All Bayes factors were interpreted using the classification scheme proposed by Jeffreys (1961). In this classification a bayes factor (i.e., BF_{10}) of 1-3 indicates anecdotal evidence for the alternative; 3-10 is substantial; 10-30 is strong evidence; 30-100 is very strong and >100 is decisive.

To assess the effect of perceived sensation on performance the present study adopted a similar approach to that of Harty et al., (2019). That is, measures of perceived sensations were summed to produce a ‘total sensation score’ for each participant in each condition, to compare the scores across stimulation conditions. A comparison for the subjective rating of how sensations affected performance in the perceptual learning task was also made across conditions.

Data and study materials are available on the Open Science Framework (osf.io/bdptx). This work was not preregistered.

Results

Figure 3 displays mean discrimination performance across exposure conditions as a function of stimulation type and trial type. Inspection of the figure suggests better discrimination performance for stimuli previously exposed on intermixed as opposed to blocked schedules (the classic *IBE*), but little apparent difference in this pattern as a function of stimulation type. A mixed factor ANOVA with within-subjects factors of exposure (intermixed, blocked, and novel), trial type (same or different), and stimulation type (anodal & sham), alongside the between-subjects factor of montage (DLPFC, PPC) was conducted. The key analysis relating to the hypothesis that anodal stimulation should disrupt perceptual learning is reported first, followed by the remainder of the analysis

There were no interaction effects for exposure type and stimulation type $F(2, 92) = 0.41, p = .662, \eta^2_p = .01$, nor any interaction involving exposure type and stimulation type. There was no significant effect for any of the three-way interactions. That is, for exposure type, trial type and stimulation type $F(2, 92) = 0.57, p = .567, \eta^2_p = .01$; nor for the interaction between exposure type, stimulation type and stimulation location $F(2, 92) = .93, p = .399, \eta^2_p = .02$. No effect for the three-way interaction between trial type, stim type, and stim location, $F(1, 46) = 3.43, p = .070, \eta^2 = .07$; and no four-way interaction between exposure type, trial type, stimulation type and stimulation condition $F(2, 92) = 0.46, p = .635, \eta^2_p = .01$.

Despite the lack of stimulation effect, the intermixed blocked effect was observed. That is, there was a main effect of exposure $F(2, 92) = 12.86, p < .001, \eta^2_p = .22$. Post hoc analysis revealed that this followed the typical pattern of intermixed exposure resulting in better discrimination performance compared with blocked ($t(46) = 3.12, p = .006$) and novel ($t(46) = 4.75, p < .001$), but no difference between blocked and novel conditions ($t(46) = 1.86, p = .162$). There was also a significant main effect of trial type indicating that same trials were more accurately discriminated compared with different trials, $F(1, 46) = 156.30, p$

$< .001$, $\eta^2_p = .77$. In addition, the interaction between exposure and trial type was significant, $F(2, 92) = 9.15$, $p < .001$, $\eta^2_p = .17$. This is entirely consistent with previous reports in the literature where performance changes following perceptual learning were seen predominantly on ‘different’ test trials (e.g., Jones & Dwyer 2013; Lavis & Mitchell, 2006, Mitchell, Nash et al., 2008). That is, performance on intermixed different trials (M: .53) was significantly higher than blocked different trials (M: .44, ($t(46) = 3.44$, $p = .006$), and novel different trials (M: .41 ($t(46) = 5.33$, $p < .001$)). There was no significant difference between blocked and novel trials ($t(46) = 1.70$, $p = .381$) and there were no statistically significant differences between same trials in the three exposure conditions (largest $t(46) = .63$, $p = 1.00$ for the difference between blocked same and novel same).

The remainder of the ANOVA revealed a main effect of stimulation location with participants who received PPC stimulation displaying better overall discrimination performance (M: .66 SE: .01) compared with those in the DLPFC stimulation condition (M: .63 SE: .01 ($F(1, 46) = 4.72$, $p = .035$, $\eta^2 = .09$)). But no other significant effects. That is, there was no main effect of stimulation type, $F(1, 46) = 0.03$, $p = .860$, $\eta^2_p = .00$, nor were there significant interactions between exposure type and stimulation location ($F(2, 92) = 2.06$, $p = .133$, $\eta^2_p = .00$); stimulation type and stimulation location $F(1, 46) = 0.11$, $p = .739$, $\eta^2_p = .00$ or trial type and stimulation location $F(1, 46) = 0.58$, $p = .449$, $\eta^2_p = .01$. There was no three-way interaction for exposure type, trial type and stimulation location, $F(2, 92) = .07$, $p = .933$, $\eta^2_p = .00$,

The key finding is that anodal tDCS does not appear to affect perceptual learning (i.e. the interactions between stimulation type and exposure schedule were non-significant). Given the effects of exposure type were predominantly carried by the different trials, focused Bayesian ANOVAs were performed on these trials using the factors of stimulation type and exposure schedule (once each for the DLPFC and PCC groups). Taking first the analysis for

the DLPFC stimulation group, an analysis of effects confirmed this pattern. There was extremely strong evidence against excluding exposure type ($BF_{\text{excl}} = 0.01$), but substantial evidence in favor of the null hypothesis for stimulation type ($BF_{\text{excl}} = 7.14$) and the stimulation type $\times$ exposure type interaction ($BF_{\text{excl}} = 14.29$).

For the PPC condition, an analysis of effects supported these findings. There was moderate evidence against excluding exposure type ($BF_{\text{excl}} = 0.27$). Conversely, there was anecdotal evidence favoring the exclusion of for stimulation type ($BF_{\text{excl}} = 2.70$) and substantial evidence against the exposure $\times$ stimulation interaction ($BF_{\text{excl}} = 6.67$).

Further analysis examined how sensations from each session of stimulation were perceived to affect performance. Unfortunately, of the 48 participants only 12 completed the post-stimulation survey for both sessions. These were all in the DLPFC stimulation condition. As such, a paired t-test was conducted to assess the difference between total sensation scores and perceived influence on performance for anodal and sham stimulation. The analysis revealed a significant difference in perceived sensations for anodal stimulation (M: 18.42 SD: 1.83) compared with sham stimulation (M: 12.92 SD: 1.24, $t(11) = 12.16$, $p < .001$, $BF_{10} = 128204$). However, there was no significant effect of perceived performance impact between anodal (M: 1.67 SD: .49) and sham stimulation (M: 1.25, SD: .45, ($W=24$, $n=12$, $p = .073$, $BF_{10} = 1.57$).

Discussion

The experiment reported here examines the potential causal role of the dorsolateral prefrontal cortex (DLPFC), and posterior parietal cortex (PPC), in human perceptual learning - as indexed by the intermixed blocked effect (*IBE*). Better discrimination performance was observed on intermixed trials compared to blocked and novel trials, but there were no observed differences between the blocked and novel (i.e., replicating the intermixed blocked effect). However, there was no evidence that exposure to similar stimuli whilst receiving anodal tDCS, to either the DLPFC or PPC, elicited change in performance for intermixed or blocked trials, compared with the sham condition. These results potentially contrast with several tDCS studies, using different indices of perceptual learning, which have found effects of stimulation on learning (e.g., Civile, Verbruggen et al., 2016; McLaren et al., 2016; Civile et al., 2021, Civile et al., 2025; Clark et al., 2012; Filmer, Dux & Mattingley, 2015; Hiraga et al 2025; Wagner et al., 2020). These present findings therefore potentially question the generality of previous observations of anodal stimulation of DLPFC and PPC on perceptual learning, and in turn, also raise potential questions about the generality of the theoretical interpretation of those prior studies.

The measure of perceptual learning used in the studies which have found anodal stimulation disrupts learning is the magnitude of the inversion effect derived from better performance with upright vs inverted exemplars (see, Civile et al., 2014; McLaren, 1997). That is, many studies have found that anodal stimulation over the left DLPFC, an area linked with attentional processes, disrupts perceptual learning as indexed by a reduction in the usual inversion effect seen with highly familiar stimuli (e.g., Civile, Verbruggen et al., 2016; McLaren et al., 2016; Civile et al., 2021, Civile et al., 2025). In these studies, participants are typically subject to three phases (pre-exposure, study and test). The first phase trains participants to categorize checkerboards (or faces) into two categories (A or B), while

receiving stimulation (anodal or sham; or, anodal or cathodal (e.g., Civile et al., 2025)). In the second phase, participants passively viewed novel exemplars from a trained category and a novel category, in either an upright or inverted orientation, and in the final phase participants are given a recognition task comprising stimuli that were novel or had been previously exposed. The studies suggest that the perceptual learning (as indexed by the inversion effect) observed in control groups was eliminated in the anodal condition. Given that stimulation occurred over the left DLPFC, an area associated with top-down processes, the finding is consistent with the role of these areas within human perceptual learning (e.g., Mundy and Dwyer 2015). While the inversion effect may be a product of expertise, and thus reflect perceptual learning, its unique features may also mean that it provides an index of only some aspects of perceptual learning and thus might not capture the full generality of perceptual learning. In particular, these prior results using inversion as the key index of learning do not appear to generalize to the schedule-dependent aspects of perceptual learning displayed in the *IBE* (at least with the current stimulation montage).

In addition, the reduction in inversion effects found in many studies have been interpreted in the context of the salience modulation aspect of MKM model, specifically it is thought that anodal stimulation effectively reduces/switches off salience modulation by removing the error-driven mechanism that, under normal circumstances, ‘boosts’ an input units’ activation. In the cases that the inversion effect has been disrupted; this stems from impaired recognition for upright stimuli. In this instance, the application of anodal stimulation is thought to disable error driven salience modulation and lead to increased generalization between previously exposed prototype-defined categories. As such common features become more prominent due to coactivation and unique features (previously thought to receive additional activation in the absence of DLPFC stimulation) now have no additional activation and therefore low salience. As a result, stimuli in the upright condition become

more difficult to discriminate because they look more similar to each other and this leads to a reduction in the inversion effect found across multiple studies (Civile, Cooke, et al., 2020; Civile & McLaren, 2022; Civile, McLaren, et al., 2020, 2021; Civile, McLaren, & McLaren, 2018; Civile, Quaglia, et al., 2021; Civile, Waguri, et al., 2020). Importantly, this salience modulation aspect of the MKM model could potentially also be considered as an account of other examples of perceptual learning. In this light, the lack of effects of tDCS stimulation in the current study may question whether salience modulation does contribute to the *IBE* effect.

To unpack this idea, for intermixed exposure, on each trial *X* (i.e., the common element) is presented and therefore becomes better predicted. This potentially results in lower salience than the unique features (i.e., *A* and *B*), which subsequently receive a boost in salience. For blocked exposure (e.g., *AX*, *AX*..., *BX*, *BX*...) repeated exposure of each stimulus leads to all features becoming good predictors, and results in a general loss of salience for these features. In the context of the current findings, if salience modulation was involved in the *IBE* then a change in performance between anodal and sham conditions should have been observed – similar to that found in the inversion-based experiments. Instead, the evidence for the absence of any difference between stimulation conditions within the *IBE* might reflect the presence of multiple contributions to PL - and so the current null result might be the product of other mechanisms (e.g., mutual inhibition between unique elements) - even if salience modulation is switched off. This is not to say that salience modulation cannot contribute to the *IBE*, merely that the *IBE* may be supported by mechanisms outside salience modulation.

That said, it should be noted there are differences in the current stimulation montage compared with the inversion studies of perceptual learning. The main difference is the duration of the stimulation and the intermittent nature of the stimulation in the present study compared to the block of stimulation in inversion demonstrations. In previous demonstrations

using inversion the duration of the stimulation, which occurs concurrently with the study phase, is 10 minutes of blocked stimulation (e.g., Civile et al., 2023). In the present study stimulation was for a total of 8 minutes, but intermittent because it occurred at the onset of each exposure, which was followed by the discrimination task whereby stimulation did not occur. This online stimulation is thought to modulate specific networks that are assumed to be involved in the task compared with offline stimulation that has been suggested to rely on modification of neuronal activity that lasts beyond the period of stimulation (see, Miniussi, Harris, & Ruzzoli 2013).

The differences in montage are an important caveat but may not alone provide an explanation as to why there have been effects observed with inversion and not with the *IBE*. Especially given that the effects of tDCS have been found to be both acute and relatively long lasting (Coffman, Clark & Parasuraman, 2014). That is, even very short DC stimulation causes a shift in resting membrane potentials under the electrode (e.g., Nitsche et al., 2005; Accornero et al., 2007; Romero Lauro et al., 2014). Indeed, there are many demonstrations of short dose stimulation, between 3-8 minutes, at the DLPFC (see review by Tremblay et al., 2014 for examples) and studies to suggest that stimulation to the PPC can effect spontaneous oscillatory brain activity during stimulation of 1–2 minutes (Mangia, Prini & Cappello 2014). These protocols are in line with early evidence that has suggested 5-7 minutes of stimulation is enough to produce lasting effects (Fricke et al., 2011; Nitsche & Paulus, 2000; Nitsche et al., 2005).

Equally, despite the differences in montage there is ample evidence that stimulation does influence learning across different tasks (see, Civile, Verbruggen et al., 2016; Clark et al., 2012). That said, it is not uncommon to find a lack of anodal effects in transcranial stimulation: several learning studies have found consistent cathodal effects, but little to no effect of anodal stimulation (reviewed in Sczensy-Kaiser et al., 2016), which is in line with

the inconsistent findings reported within reviews of non-learning tasks focusing on DLPFC and PPC (see, Lavezzi et al., 2022; Tremblay et al., 2014). Thus, future studies should consider investigating the *IBE* using cathodal stimulation at the DLPFC and PPC before it is concluded that these regions do not play a causal role in perceptual learning and the *IBE*.

Notwithstanding the stimulation differences, the current study does raise questions about the contribution of different classes of account and whether the discrimination improvements produced by perceptual learning can be attributed theories reliant on memory and or attentional processes or accounts that rely on stimulus-centered mechanisms. One of the key motivations for using stimulation to investigate learning effects is a lack of behavioral evidence to determine the most useful account for explaining the results of many studies using the *IBE* (see, Dwyer & Mundy, 2015) – namely because most of the experimental findings can be explained by multiple theories (see, Mitchell & Hall 2014 for a review). While the present study does not provide definitive evidence for one class of account over others it does potentially raise some questions about attentional and memory processes given the lack of evidence for both DLPFC and PPC involvement in the *IBE*, which appears inconsistent with the fMRI studies of this effect (i.e., Mundy et al., 2009; 2014) – although this should be considered tentative pending future studies using cathodal stimulation and/or different stimulation montages.

This is further complicated by the notion that mechanisms of cortical involvement in learning might be task-dependent and dynamic across time (e.g., Mundy 2014; Nydam, Sewell and Dux, 2020). For example, Nydam, Sewell & Dux, (2020) found that cathodal stimulation to the left PPC did not affect visual statistical learning (VSL) when measured in an offline (i.e., receiving stimulation before the task) recognition task (Exp 1). However, using an online (i.e., receiving stimulation during the task, or part of the task) task (i.e., Exp 2) active tDCS significantly expedited learning. This contrasts with our findings that anodal

online tDCS to the PPC did not affect learning performance relative to sham, which potentially suggests the lack of attentional/memory processes involved in the intermixed blocked effect – despite fMRI evidence to the contrary (e.g., Mundy et al., 2009; 2014). But as noted above, such a conclusion should be considered tentative until confirmed using cathodal stimulation and/different stimulation montages given previous studies, like Nydam et al. (2020) used cathodal stimulation. Equally, preliminary data from a study investigating the intermixed blocked effect found a significant effect of cathodal stimulation to the occipital cortex on blocked performance (Jones, Dwyer & McGonigle, 2023). In this demonstration anodal stimulation did not significantly modulate performance compared to sham. It could be that task performance is insensitive to anodal stimulation.

In summary, the present study potentially raises questions about the generality of previous observations of anodal tDCS impairment of perceptual learning (e.g. Civile et al., 2023). That is, it is possible that such stimulation may reliably disrupt inversion effects based on expertise, but may not impact on all examples of perceptual learning. In addition, the present results raise the possibility that there may be a lack of causal contribution to perceptual learning as indexed by the *IBE*, from the DLFPC and PPC brain regions linked to top-down perceptual mechanisms (e.g., Mundy et al., 2014). This is a counterpoint to the work of other labs, which has indicated that inversion effects stemming from perceptual learning are indeed influenced by brain regions linked to more top-down processes (e.g., Civile, Verbruggen et al., 2016). Taken together, these findings might tentatively suggest that separable processes are involved in different indexes of perceptual learning with the inclusion of *IBE* providing an important addition to the brain stimulation and perceptual learning literature. However, all of these conclusions should remain tentative pending further work using different stimulation montages. Moreover, the limitations of the current understanding of the tDCS manipulations should be noted. In particular, the specificity of the brain regions

involved, the type of stimulation used, and the timing of the manipulation effects, remain to be determined. These issues can be addressed using a combination of computational modelling, individualized head models and simultaneous neuroimaging (Soekadar, Herring and McGonigle, 2016) to better target and understand the effects of stimulation on brain regions involved in perceptual learning.

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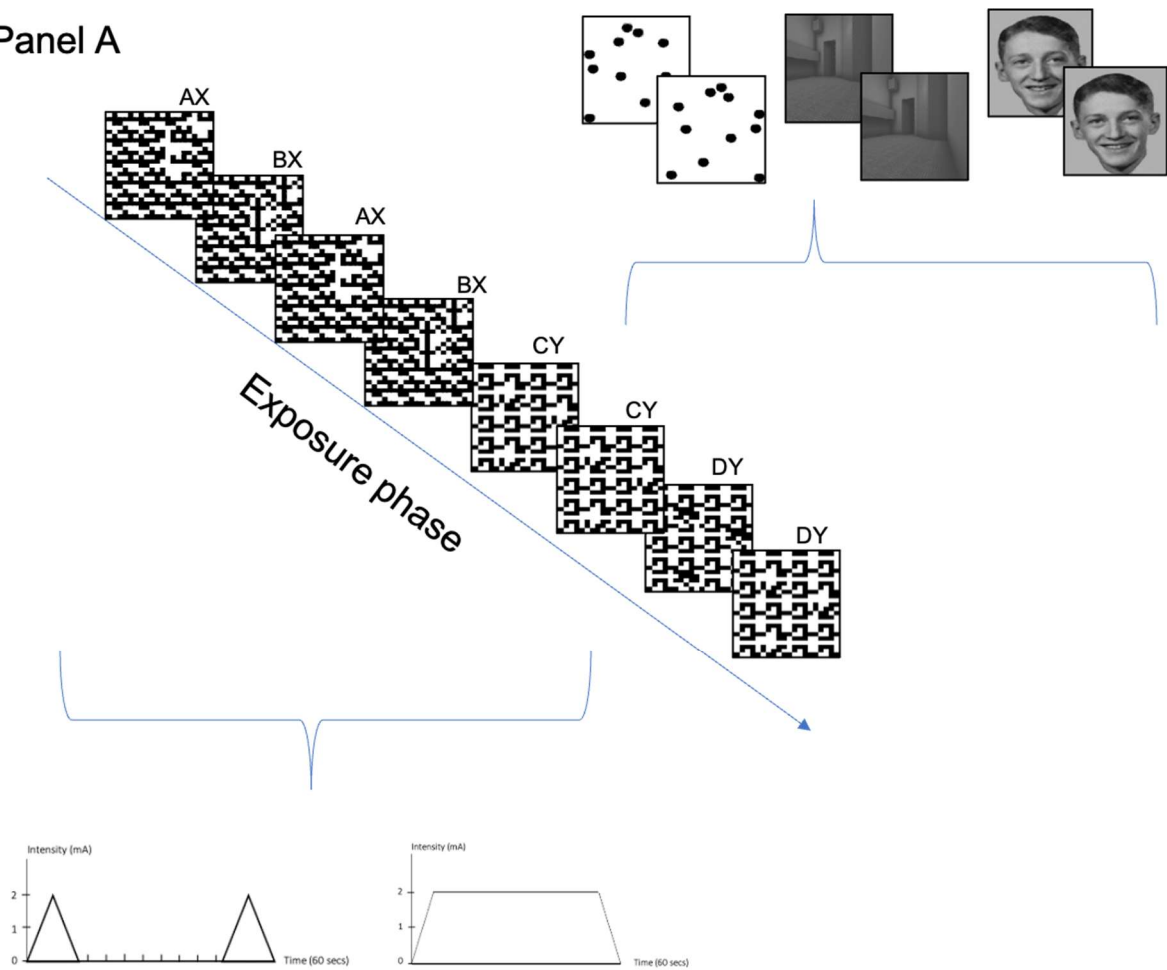
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Figure 1:

Panel A



Panel B

Discrimination task

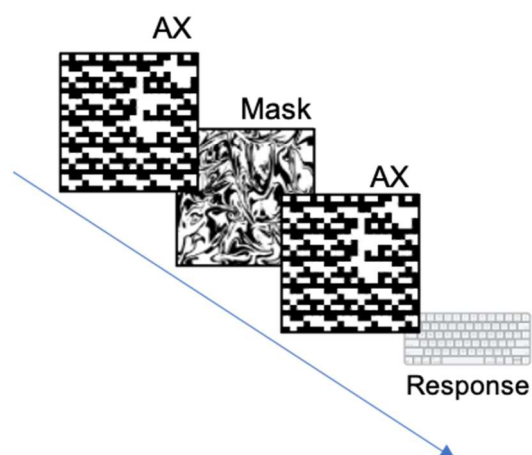


Figure 2:

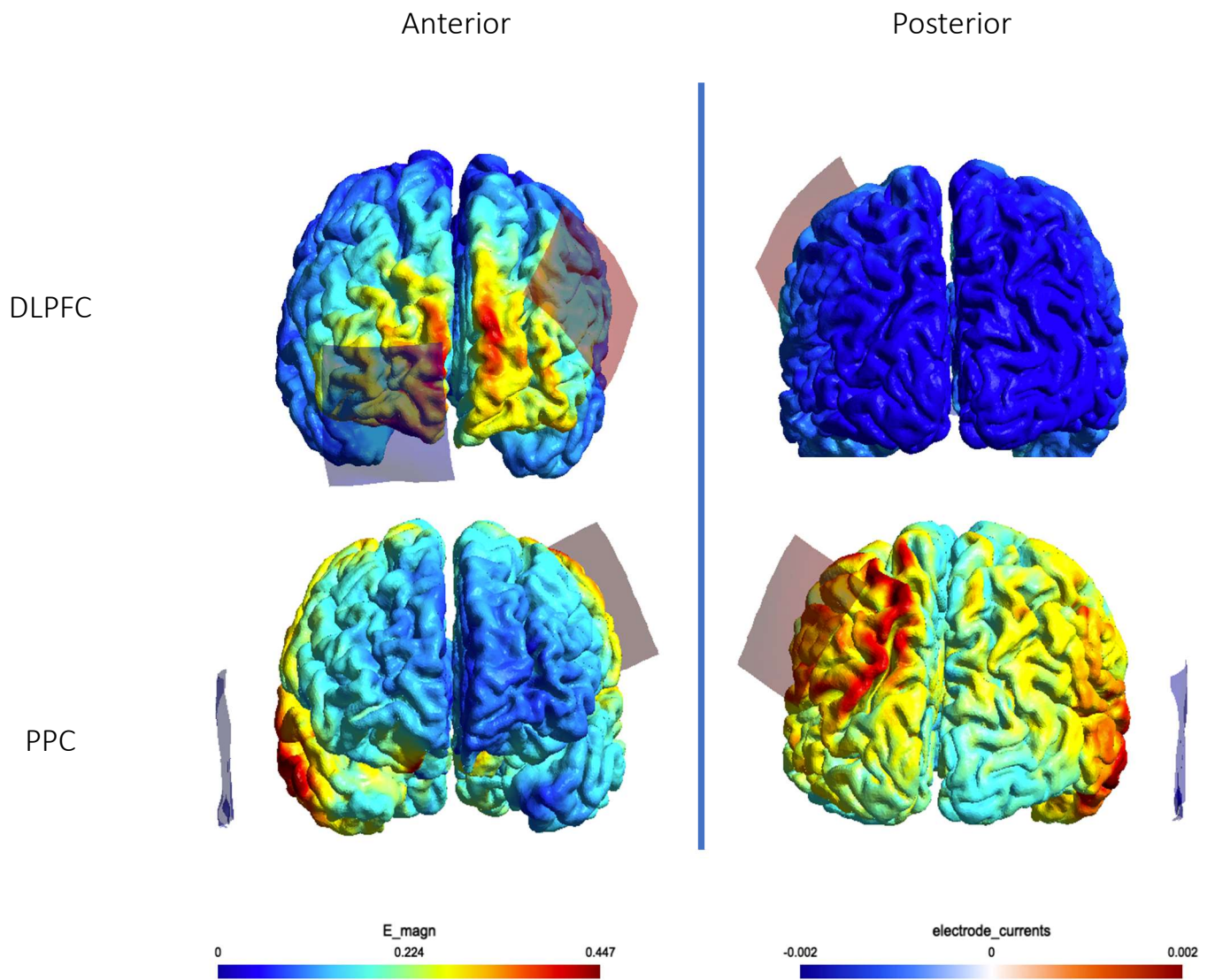


Figure 3:

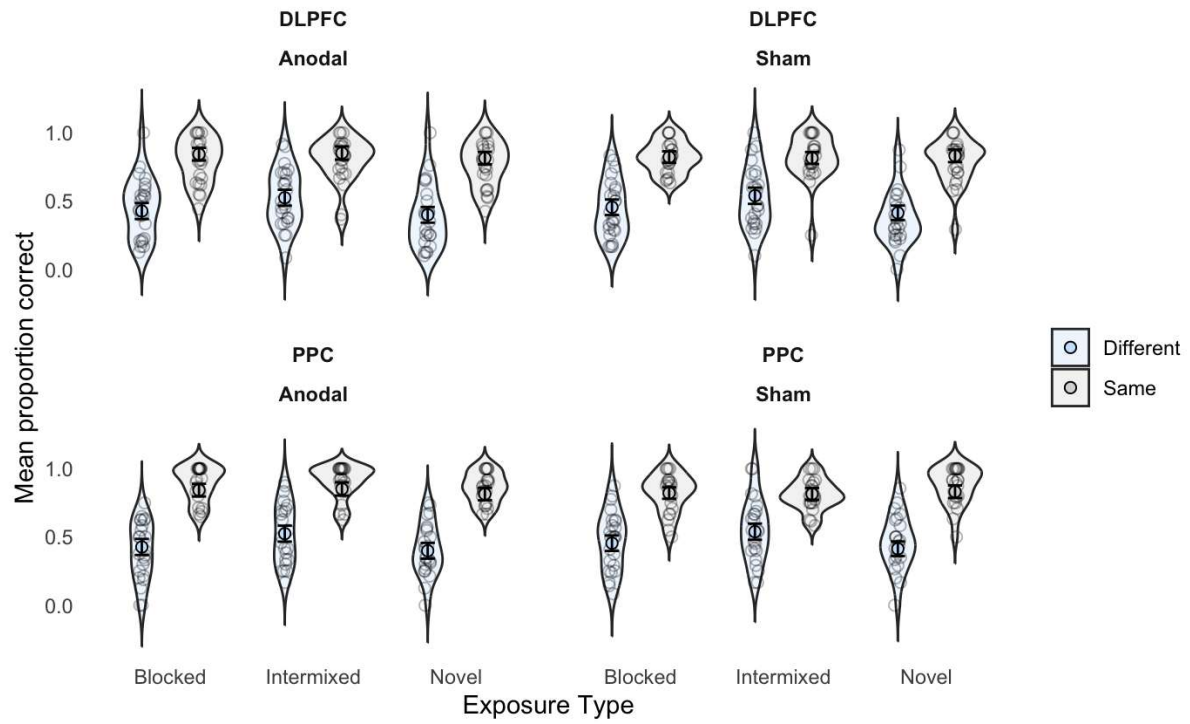


Figure captions:

Figure 1: A schematic representation of an exposure phase and discrimination test trial. Panel A) represents a 60 sec exposure phase during which the participant receives either sham (left) or active (right) stimulation, illustrated below. Types of stimuli used throughout the experiment are displayed above. Panel B) displays a ‘same’ test trial whereby the correct response is same. Note borders around stimuli were visible to participants during trials and are only present to highlight the stimuli. This design was repeated 8 times (i.e., twice each per stimulus class (dots, checkerboards, faces, and scenes)).

Figure 2: Current flow modelling for the two electrode montages used. The top panel (left to right) displays current flow for stimulation to the dorsolateral left prefrontal cortex for the anterior and posterior views. The bottom panel (left to right) displays the current flow for stimulation to the left posterior parietal cortex.

Figure 3: A violin plot displaying data distributions for each exposure condition as a function of trial type, anode location and stimulation condition. The black lines indicate mean performance.