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Effects of tDCS on visual statistical learning

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ABSTRACT

Visual statistical learning describes the encoding of structure in sensory input, and it has important consequences for cognition and behaviour. Higher-order brain regions in the prefrontal and posterior parietal cortices have been associated with statistical learning behaviours. Yet causal evidence of a cortical contribution remains limited. In a recent study, the modulation of cortical activity by transcranial direct current stimulation (tDCS) disrupted statistical learning in a spatial contextual cueing phenomenon; supporting a cortical role. Here, we examined whether the same tDCS protocol would influence statistical learning assessed by the Visual Statistical Learning phenomenon (i.e., Fiser and Aslin, 2001), which uses identity-based regularities while controlling for spatial location. In Experiment 1, we employed the popular exposure-test design to tap the learning of structure after passive viewing. Using a large sample (N = 150), we found no effect of the tDCS protocol when compared to a sham control nor to an active control region. In Experiment 2 (N = 80), we developed an online task that was sensitive to the timecourse of learning. Under these task conditions, we did observe a stimulation effect on learning, consistent with the previous work. The way tDCS affected learning appeared to be task-specific; expediting statistical learning in this case. Together with the existing evidence, these findings support the hypothesis that cortical areas are involved in the visual statistical learning process, and suggest the mechanisms of cortical involvement may be task-dependent and dynamic across time.

Through repeated experience, the human brain can form implicit knowledge about complex patterns in the sensory environment (Fiser and Aslin, 2001; Turk-Browne, 2014). This ability, known as statistical learning, has been observed across a variety of task domains (Kirkham et al., 2002; Perruchet and Pacton, 2006; Conway and Christiansen, 2005) that vary in terms of the stimulus dimension (i.e., visual, auditory and language), the type of regularities (i.e., sequential, spatial or graph-based regularities) and their relational components (i.e., adjacent or non-adjacent probabilities). This ubiquitous nature of statistical learning has led to the proposal of a domain-general neural mechanism for encoding structure based on experience (Fiser and Lengyel, 2019; Perruchet and Pacton, 2006; Reber, 1989). In support of this idea, there appears to a common list of brain regions in which activity correlates with detecting regularities across various task domains (for a review, see Batterink et al., 2019). Recent brain stimulation evidence has clarified the involvement of frontoparietal regions in the visual statistical learning process (Nydam et al., 2018; Rosero Pahi et al., 2020). Yet the nature of this involvement across tasks that are believed to tap the same underlying process requires further investigation.

1. Statistical learning in visual scenes

An important function of statistical learning concerns our ability to swiftly recognize visual scenes. After one repetition of a scene, visual processing is biased by knowledge about how objects and features were arranged in space and time (Biederman et al., 1982; Friedman, 1979; Henderson et al., 1999). In their seminal work, Fiser and Aslin (2001) demonstrated how the recognition of familiar scenes was based on automatic encoding of statistical regularities between objects. The way they measured this was by having participants view a series of spatial arrays that contained abstract shapes arranged in a grid. Unbeknownst to observers, each shape belonged to a base pair that had a fixed spatial arrangement over the course of the experiment. The shapes were recombined in all possible ways such that the base pairs were only recognisable based on having a higher joint probability than other coincidental shape-pair events. In a forced-choice recognition test, observers reliably selected the base-pairs over foil pairs (Fiser and Aslin, 2001). Since observers were not aware that any learning had taken place, the knowledge was said to be implicit. Above-chance recognition in the Fiser and Aslin task is taken as evidence that the encoding of visual

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objects is based on statistical characteristics beyond mere frequency alone. In subsequent experiments, the same authors showed humans can extract multiple higher-order statistics in parallel and can do so without an active task or feedback (Fiser & Aslin, 2002a, 2005). This led to terms such as "incidental" and "spontaneous" being used to describe the statistical learning process. The spontaneous Visual Statistical Learning effect been used repeatedly in other work since (Conway et al., 2007; Covington et al., 2018; Karuza et al., 2017; Luo and Zhao, 2017; Roser et al., 2015; Schapiro et al., 2014; Zhao et al., 2011) to capture the statistical learning process in vision.

Following this pioneering work, a variety of paradigms were developed to tap the learning of structure in spatial arrays (Fiser and Aslin, 2002b; Orbán et al., 2008; Turk-Browne, Johnson, Chun and Scholl, 2008b). While some have followed the exposure-test deign to measure all-or-none learning after passive exposure, others have employed a cover-task to track behavioral performance throughout the learning period (Turk-Browne, Johnson, Chun and Scholl, 2008b). Popular among these has been the contextual cuing task (e.g., Chun and Jiang, 1998); possibly due to its ability to assess the effects of statistical learning on behaviour that is distinct from learning of stimulus-response patterns alone (i.e., SRT tasks).

In the standard contextual cuing paradigm, observers perform a visual search task and make a forced-choice response about a target feature (e.g., its orientation). In half the search arrays, the position of items is random across the blocks, and so search performance becomes faster over time; in line with procedural learning in visual search. In the other half of arrays, the position of items is fixed across blocks such that the arrays come to predict a target location, which speeds search performance compared to the control condition. This benefit is known as the cuing effect. Importantly, because the fixed arrays do not predict the target response, only the target location, the learning in contextual cuing is distinguished from other purely motor or perceptual learning paradigms (i.e., SRT tasks). Contextual cuing is believed to track the formation of statistical learning about relationships in the visual scene (Chun and Turk-Browne, 2008; Goujon et al., 2015). Thus, both the Visual Statistical Learning effect and the Contextual Cuing task represent two prominent, but distinct, ways to tap a common statistical learning process in spatial vision. Both tasks have also featured in the neuroimaging work.

2. Neural correlates of visual statistical learning

The neural substrates of statistical learning involve a distributed network of cortical, subcortical and sensory regions. This network is likely to include both modality-specific and domain-general mechanisms (for a review, see Batterink et al., 2019). In one case, there is strong evidence to suggest that hippocampal involvement reflects a domain-general role of the long-term memory system (Schapiro et al., 2012; Schapiro et al., 2016). In another case, the activation of sensory regions (e.g., visual, auditory, somatosensory) appears domain-specific, with select regions only performing computations for the respective input modalities (Frost et al., 2015; Conway and Christiansen, 2006). A growing body of evidence reveals that high-level processing areas in frontal and parietal regions are activated across a variety of input domains. For example, activity in the left IFG (i.e., "Broca's area") is correlated with statistical learning in the language domain (Cunillera et al., 2009; Karuza et al., 2013), the auditory domain (Abla et al., 2008) and the visual domain (Turk-Browne and Scholl, 2009); supporting the notion that higher-cortical involvement may be somewhat domain-general (Fedorenko et al., 2012). Such a role would be consistent with the broader functions of these cortical regions in a range of complex behaviours and cognitive operations.

Learning sequential relationships in the Serial Reaction Time (SRT) task has undergone much investigation (Abla et al., 2008; Aly and Turk-Browne, 2016; Gheysen et al., 2010; Turk-Browne et al., 2008b; Turk-Browne et al., 2010). Learning in sequence tasks, either motor or visual, is associated with activity in prefrontal, motor and striatal regions; consistent with the role of a procedural motor learning network. But SRT tasks cannot dissociate the learning of statistical regularities from the learning of visuo-motor response patterns. The neuroimaging evidence from learning spatial regularities can more readily be distinguished from motor-response learning.

Statistical learning of spatial regularities has been associated with activation in the left frontoparietal region across different task domains. Using the contextual cuing task, there is consistent evidence that processing spatial structure evokes BOLD activity changes in the left inferior parietal sulcus (IPS), the superior parietal lobe (SPL), the temporal parietal junction (TPJ) and the medial prefrontal cortex (mPFC; Giesbrecht et al., 2013; Hall et al., 2018; Manginelli et al., 2013; Pollmann, 2012; Pollmann and Manginelli, 2010). Similarly, the passive Visual Statistical Learning effect is associated with evoked activity in frontoparietal regions, particularly in the left SPL (Karuza et al., 2017).

Moving beyond region-based activity, functional network changes may also be important for visual statistical learning. During the contextual cuing task, early activity changes in the IPS predicted the size of the cuing benefit across individuals (Manginelli et al., 2013), suggesting a functional relationship between parietal activity and learning outcomes. Likewise, during passive exposure in the Fiser and Aslin task, connectivity dynamics correlated with learning outcomes at test (Karuza et al., 2017). More specifically, a portion of the superior parietal lobe (in the left precuneus) and the lateral occipital cortex (LOC) decreased connectivity with frontal regions early on, and this predicted greater recognition of the pairs. Weakened connectivity in a parietal-hippocampal network was also observed during exposure to regularities during a search task in contextual cuing (Manelis and Reder, 2012). Together, this evidence builds a case for the intervening role of frontal and parietal regions in the visual statistical learning process across task settings. Yet it falls short of testing the hypothesis directly. It remains unclear whether the evoked frontoparietal activity in fMRI studies reflects concurrent processes that act on the task material or a processes that directly contributes to learning. To settle these issues, causal manipulations of brain activity during the learning period are warranted.

2.1. Applying causal neuromodulation methods

Experiments using tDCS can uncover causal brain-behaviour links that govern cognitive operations and behaviour (Filmer et al., 2014). The technique involves placing two rubber electrodes on the scalp and delivering a weak electrical current to a targeted brain region. The stimulation is hypothesized to act on membrane potentials to modulate the net likelihood of neural activity in a given target region or network (Bikson and Rahman, 2013; Dayan et al., 2013; Filmer et al., 2014; Nitsche and Paulus, 2000; Nitsche, Schauenburg, et al., 2003b). Unlike TMS, tDCS cannot directly evoke action potentials (Ruhnau et al., 2018). Instead, the induced current interacts with the state of the cortex at the time of stimulation to alter the functional output of a given neural circuit (Bikson and Rahman, 2013; Bortoletto et al., 2015). Therefore, by combining tDCS with a task one can perturb a target network in a given state in order to provide causal evidence regarding the neural mechanisms that govern cognition and behaviour. This approach has been successfully applied in the domains of motor learning (Nitsche, Schauenburg, et al., 2003b; Reis et al., 2009) and cognitive training (Filmer, Lyons, Mattingley and Dux, 2017a; Filmer et al., 2013; Filmer, Varghese, Hawkins, Mattingley and Dux, 2017b) where delivering tDCS over key processing regions during training not only altered the learning behaviour but did so by modulating an underlying cognitive process; namely memory consolidation in the case of motor learning (Reis et al., 2009), and evidence accumulation in the case of decision-making training (e.g., Filmer et al., 2017b). Whether similar effects may be observed for implicit forms of learning has undergone only limited investigation.

Previously, and in the first study of its kind, we delivered tDCS during a spatial contextual cuing task to investigate the involvement of cortical regions in the statistical learning process (Nydam et al., 2018). Across six experimental groups, tDCS was used to modulate activity in either the left posterior parietal cortex or the left prefrontal cortex using anodal, cathodal or sham stimulation. In the sham groups, a cuing benefit appeared early and was maintained throughout the task. In the cathodal groups, the early cuing effect was disrupted, suggesting that stimulation delayed the statistical learning process. This cathodal effect was observed for both the frontal and parietal target regions (Nydam et al., 2018). The result was taken as evidence that frontoparietal regions are involved in the visuo-spatial statistical learning process, consistent with the fMRI work.

Based on the evidence to date, it appears that parietal regions may be particularly important for statistical learning in spatial arrays. While both contextual cuing and visual statistical learning tasks recruit frontal and parietal regions, only the parietal region has been linked to functional changes that predict implicit learning behaviour in both cases (i.e., either via the parietal-hippocampal network or the frontoparietal network; Karuza et al., 2017; Manelis and Reder, 2012; Manginelli et al., 2013). A substantial body of research indicates the parietal cortex is part of a multi-demand (MD) network recruited across a range of cognitive domains (Duncan, 2010). In particular, the MD network involves a specific set of prefrontal and parietal hubs, including the cortex around the IPS, that comprise larger modules associated with cognitive demands related to memory, attention and knowledge (Dosenbach et al., 2007; Duncan and Owen, 2000). The region of cortex around the IPS represents a connector hub that has many functional linkages to other interconnected modules, including the frontoparietal control network, the saliency network and the memory retrieval network (Bertolero and Basset, 2019). Frontoparietal circuits also interact with one another in a time-varying manner to adapt brain function in support of behaviour (Bassett et al., 2015; Bassett and Mattar, 2017). This circuitry makes the frontoparietal network well placed to govern a cortical mechanism that is important for the way statistical learning effects behaviour across types of tasks. Here, we sought to investigate the modulatory effect of tDCS on statistical learning using a different task than before, but one that is believed to tap the same underlying process, namely visuo-spatial statistical learning.

2.2. Current study

In two pre-registered experiments, we explored whether tDCS over the left posterior parietal cortex (PPC) would alter learning in the Visual Statistical Learning task. Building on the previous work (i.e., Nydam et al., 2018), we focused on the effect of cathodal currents compared to an orbitofrontal (OF) control region (in Experiment 1) and to a placebo control (in Experiment 1 and Experiment 2). Our hypothesis was that if the stimulation protocol influenced a domain-general statistical learning process, the cathodal effect would generalize to a new task believed to tap the same underlying process. Therefore, there was no clear reason to include an anodal condition in the present study. Given the resource-intensive nature of this research, in Experiment 2 we focused on having a double-blind-placebo-control design. Based on the observation that activity changes in the SPL (Karuza et al., 2017; Manelis and Reder, 2012) and the IPS (Manginelli et al., 2013) have been associated with learning outcomes previously, we predicted that active tDCS over the left PPC region would modify recognition in Experiment 1; either by increasing or decreasing pair recognition compared to sham (non-directional hypothesis). If the tDCS effect was specific to our target region, we predicted the left PPC group would differ from the OF control group (non-directional hypothesis). Although the previous study on contextual cuing found a reduction in statistical learning by cathodal tDCS, the activity-dependent hypothesis (i.e., Bikson and Rahman, 2013; Bortoletto et al., 2015; Batsikadze et al., 2013) asserts that the same direction of behaviour change would not be predicted when using a different task (see Filmer et al., 2014). Any interaction between tDCS and statistical learning will provide evidence that cortical regions are involved in the statistical learning process.

3. Method

3.1. Preregistration

The design, hypotheses, and analysis plan were logged prior to data collection, and the materials and data have been made available online at: DOI 10.17605/OSF.IO/Y34XZ.

3.2. Participants

We recruited 150 healthy participants aged 18–40 years from The University of Queensland community (mean age = 21.1 years, 63% female, 66% glasses or contact use; mean Oldfield (1971) handedness score = 86%). Using a custom MATLAB script, participants were randomly assigned one of three stimulation groups: the PPC group, the sham group (placebo control) and the OF group (active control). The participants were right-handed, with normal or corrected-to-normal vision and were eligible to receive non-invasive brain stimulation according to the international safety guidelines (Nitsche et al., 2008). All provided informed written consent prior to participating and received AU$20 for attending a 1-h session. The study was approved by The University of Queensland Human Research Ethics committee.

3.3. Deviations from preregistration document

The sample size of 40 per group was based on power calculations that indicated 38 participants would be sufficient to achieve 85% power to detect a medium effect size (Cohen's d = 0.5) with alpha .05. Due to an error with the randomization script, 50 individuals were assigned to the sham group. Once realized, the sample size was amended to be 50 per group and logged in the preregistration document.

3.4. Visual statistical learning task

3.4.1. Apparatus

Participants were seated approximately 63 cm from a 19″ CRT monitor (resolution 1024 × 768; 100 Hz refresh rate) connected to an Apple iMac computer and a Macintosh keyboard. The experiment was run using custom code programmed in MATLAB 2015b using the Psychophysics Toolbox 3 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). Due to constraints in lab availability, a portion of participants were run in a different room that used a 24″ ASUS nVidia LCD monitor (resolution 1920 × 1080, 60 Hz refresh rate) connected to the same computers. Stimuli were adjusted to keep the same visual angle. There was no difference in learning based on monitor type or room.

3.5. Exposure phase

The methods for the visual statistical learning task followed those developed by Fiser and Aslin (2001; Experiment 2). As shown in Fig. 1, visual displays contained black shape-silhouettes (3.6° visual angle) arranged in an invisible 3 × 3 grid (16° visual angle) presented on a grey background (RGB: 80, 80, 80). For each participant, 12 shapes were randomly selected from the pool of 24 shapes used previously (Fiser & Aslin, 2001, 2002b) and each shape was assigned to one of six base pairs with a fixed spatial arrangement; horizontal, vertical, or oblique (left or right oriented). Each array contained one pair from each spatial arrangement, which formed eight possible pair combinations. These were then recombined in all possible cell locations within the grid to create 144 trials. Exposure trials began with a fixation dot shown for 1000 ms (with up to 500 ms jitter), followed by the stimulus shown for 2000 ms. Since no responses were required during the exposure phase,

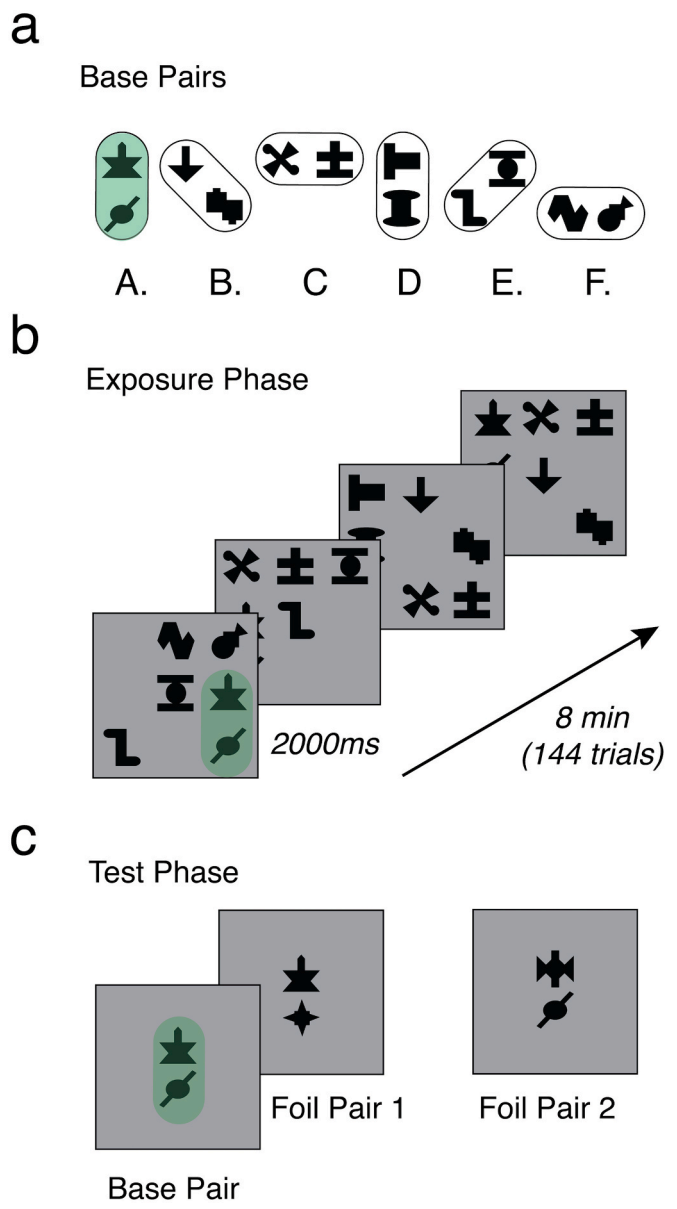

Fig. 1. The Visual Statistical Learning paradigm followed the method of Fiser and Aslin (2001). (a) Each spatial array contained three base pairs (i.e., A, B, C, D, E, F). (b) During exposure, participants viewed 144 arrays over the course of 8 min with passive viewing. (c) During the test phase, participants were shown two pairs, presented sequentially, and had to select the more familiar pair. Each base pair was compared to two foil pairs, and with counterbalanced order to form 24 test trials. Note the green shading was included here for emphasis and was not part of the stimulus. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

participants were simply instructed to view the slideshow with eyes open and to be awake. Exposure lasted 8 min and there was a self-paced break at the half-way point where participants pressed the space bar to continue.

3.6. Test phase

After exposure was the surprise recognition test. For each trial, two pairs were shown sequentially and at fixation. After the second pair, participants indicated whether the first or second pair was more familiar using index fingers to press the 'z' and 'm' keys. Participants were instructed to focus on accuracy. Each of the six base pairs were compared against two foil pairs in a counterbalanced order. This produced four recognition trials for each base pairs (24 trials total). Each test trial begin with a fixation dot for 1000 ms, followed by the first pair for 2000 ms, a blank ISI of 1000 ms, the second pair for 2000 ms, and a prompt screen with the key mappings that terminated upon response. The test lasted 2 min on average.

3.7. Transcranial direct current stimulation

3.7.1. Stimulation parameters

In a between-subjects design we manipulated: (1) the type of stimulation; either cathodal (active) or sham (placebo); (2) and the target region; either the left posterior parietal cortex (PPC) or the left orbital frontal cortex (OF: active control). To target the left PPC, the cathodal electrode was placed over the CP3 location according to the international 10–20 EEG system, and the return electrode was placed over the contralateral (right) mastoid bone. To target the orbitofrontal (OF) control region, we positioned the active (cathodal) electrode just above the left eyebrow in line with the outer edge of the eyebrow, and used the same return electrode location. The orbitofrontal cortex was chosen as the control region because it has not been associated with statistical learning in the fMRI work.

Stimulation was delivered via a Neuro-Conn stimulator connected to 5 cm × 5 cm rubber electrodes secured to the scalp with Ten20 conductive paste. For the active groups, stimulation was delivered at 0.7 mA intensity for 15 min, plus an additional 30 s ramp up and ramp down (900 s total). We chose this stimulation protocol based on Nydam et al. (2018). It produced a maximum current density of 0.028 mA/cm^2 under each electrode, well within the safe limits (Nitsche, Liebetanz, et al., 2003a). Sham stimulation involved 30 s of constant current plus a 30 s ramp up and ramp down (90 s total). To ensure adequate contact of the electrodes, the scalp was lightly abraded with alcohol wipes to remove oil and dirt, and stimulation only went ahead if an impedance below 20 kOhm could be achieved.

3.7.2. Current-flow modelling

Current-flow modelling was conducted apriori using HD-Explore software (Soterix Medical) to confirm distinct cortical electrical fields were produced by our two electrode montages. For the PPC montage, the estimated field-intensity was concentrated in the intra parietal sulcus (IPS) within the left posterior parietal region (Brodmann Area 7) with the current directing up and outward. This was distinct to our control montage targeting the OF region, for which the modelling showed concentrated currents in the anterior frontal region (Ba9 and Ba10), the ventromedial frontal gyrus (Ba25), and the inferior frontal gyrus (Ba45 and Ba47).

3.8. Procedure

Participants completed the Visual Statistical Learning task online, during tDCS. Before commencing the task, the stimulation was allowed to ramp up for 30 s, and stimulation never finished before a participant had completed all trials in the recognition test. Afterwards, participants were asked to self-report: (1) whether they recognised any shape patterns during the exposure phase, (2) whether they noticed the existence of shape pairs during exposure, (3) and to guess whether they were in the active stimulation condition or the placebo condition.

3.9. Data analysis

Our primary DV was accuracy on the familiarity test, indexed as the mean proportion correct. Frequentist statistics were computed using two-tailed tests with an alpha of .05. When calculating the Bayes Factors, we considered three relevant factors: (a) non-equal difference between groups, based on our non-directional hypotheses; (b) a small effect size, based on the previous tDCS literature; (c) and a large credible

interval, since we could not estimate an effect size with much precision we permitted. As such, we chose an uninformative prior; a zero-centred Cauchy distribution with a scale of 0.7. To interpret the Bayes Factors we employed Jeffrey's classification scheme (Wagenmakers et al., 2017). Values greater than three indicated moderate evidence in favour of the alternate hypothesis relative to the null hypothesis. Values less that one third indicated moderate evidence in favour of the null relative to the alternate. Values between one third and three indicated inconclusive evidence given the data. Finally, to assess learning in each group separately, we built null distributions to characterize chance performance and compared the observed mean to the 95th percentile. To build the null distributions, individual accuracy scores at test were converted to a deviance score f (i.e., 65% accuracy becomes +15% deviance), randomly assigned a sign (+or -) and then the mean was calculated over 1000 samples.

4. Results

4.1. Planned analyses

4.1.1. Learning across the groups

All three groups performed above chance (i.e., 50%) on the recognition test (Fig. 2). Accuracy was highest in the PPC group ($\mu = 62.90\%$, $\sigma = 9.6$, SEM = 0.14), followed by the Sham group ($\mu = 60.60\%$, $\sigma = 13.3$, SEM = 0.19), followed by the OF group ($\mu = 58.80\%$, $\sigma = 12.9$, SEM = 0.18). Learning was robust in all three groups, since the null distribution tests revealed performance well above the 95th percentile cut-off. For consistency with the visual statistical learning literature, we computed one-sample *t*-tests to compare performance to chance (50%). All were significant at $p < .001$ ($t_{(49)} = 9.471$, 5.631, and 4.854 for PPC, Sham and OF respectively). In the sham group, half the participants had the PPC montage and half had the OF montage. We checked there were no differences in recognition based on montage, and observed evidence favouring the null hypothesis, $t_{(48)} = 0.132$, $p = .896$, $BF_{10} = 0.287$ (log $BF_{10} = -1.248$).

4.1.2. Stimulation effects on learning

Having established robust recognition in all three groups, we turned to our hypothesis regarding the effect of stimulation on learning. There was no such effect. According to an independent *t*-test, pair recognition did not differ between the PPC group and the sham group, $t_{(98)} = 1.00$, $p = .318$, $d = 0.201$, $BF_{10} = 0.330$ (log $BF_{10} = -1.1$), indicating no effect of active stimulation, although the data provided only weak support for the null hypothesis over the alternate hypothesis. The control group (OF) was no different from the sham group, $t_{(98)} = -0.669$, $p = .505$, $d = -0.134$; $BF_{10} = 0.259$ (log $BF_{10} = -1.349$), indicating there was no effect of the control stimulation site, with moderate support favouring the null hypothesis. The difference between the PPC and OF groups was not significant, with the data in the uninformative range; $t_{(98)} = 1.795$, $p = .076$, $d = 0.359$, $BF_{10} = 0.897$ (log $BF_{10} = -0.129$). Overall, these results indicated the data were insufficient to determine any reliable group differences, though trended towards a null effect of stimulation.

4.2. Exploratory analyses

4.2.1. Removal of non-learners

Despite robust learning at the group level, a portion of participants failed to recognize the pairs above chance (14% of the total sample). This was compatible to the broader VSL literature in which roughly one third of people do not show the learning effect (Arciuli et al., 2014; Siegelman et al., 2017; Turk-Browne and Scholl, 2009; Turk-Browne et al., 2005). As such, some have argued that a more representative measure of learning would be the total number of individuals who exhibit above chance performance (Siegelman et al., 2017; Siegelman et al., 2016). A chi-squared test on the number of non-responders indicated no group differences (four in the PPC group, six in the Sham group, and 11 in the OF group), $\chi^2 = 4.319$, $p = .115$; $BF_{10} = 1.699$. Since our main hypothesis concerned *learning* we removed these individuals and computed a one-way ANOVA on mean accuracy, since this test is robust to differences in sample size. The group effect was not significant, $F_{(2, 126)} = 0.108$, $p = .898$, $BF_{10} = 0.082$ (means: PPC: 64.4% > Sham: 63.4% > OF: 63.8%), and the data strongly favoured the null hypothesis over the alternative. This exploration revealed that constraining the analysis to learners did not change the pattern of null results. Arguably it led to proportionally stronger support for the null over the alternative.

4.2.2. Self-report awareness

Upon questioning, 59 individuals (39%) reported that they were aware of pairs in the exposure phase. By this measure, fewer people were aware in the OF group (26%), followed by the PPC group (42%), followed by the Sham (50%) group. A chi-squared test revealed significant differences across the groups, $\chi^2 = 6.258$, $p = .044$, $BF_{10} = 2.503$. Subjective awareness related to recognition as you might expect, with higher accuracy in the aware individuals (65.5%) compared to those

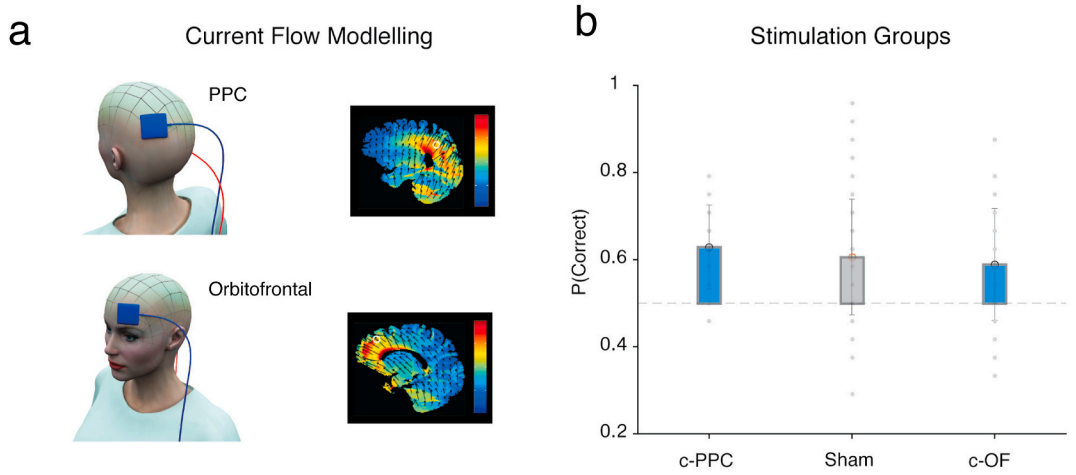

Fig. 2. (a) Current flow modelling shown for the two electrode montages used to target the left PPC, as the region of interest, and the left OF cortex, as the active control region. For the sham stimulation (not shown), half the group had the electrodes applied in the PPC montage and half had them applied in the OF montage. (b) Accuracy on the recognition test across the stimulation groups, with the individual data shown in dots and mean data shown in bars. The horizontal dotted line represents chance performance (50%) and the error bars indicate the standard error of the mean. All three groups were above chance but there were no group differences.

unaware (57.7%), $t_{(148)} = -4.084$, $p < .001$, $BF_{10} = 285.4$, and this difference was highly reliable. Critically, when investigating the possible interaction between awareness and stimulation on accurac, a two-way ANOVA revealed no Awareness × Group interaction, $F_{(2, 144)} = 0.546$, $p = .580$, $BF_{10} = 0.185$, with strong support for the null hypothesis over the alternate. So while fewer people reported being aware in the orbitofrontal stimulation group, the (null) effect of stimulation on accuracy did not depend on awareness.

5. Discussion

In Experiment 1, we used the seminal Visual Statistical Learning paradigm (Fiser and Aslin, 2001) to assess passive encoding of statistical cues in spatial scenes. The results indicated robust learning of the embedded structure, but no effect of stimulation on this learning. These findings stand in contrast to our predictions that were guided by the cathodal effect observed for spatial context learning (Nydam et al., 2018). There are two reasons why we may have failed to observe a stimulation effect in this study. The first pertains to how the learning was measured.

By asking observers which pair was more familiar at test, the Fiser and Aslin paradigm involves an overt familiarity judgment. Some authors have noted the limitations of using explicit tests to gauge implicit knowledge (Turk-Browne et al., 2005), suggesting they may tap conscious knowledge which is stimulus-specific (Turk-Browne, 2014) and distinct from implicit knowledge which involves integration across stimuli (Thiessen et al., 2013). In harmony with this idea, experimental work has demonstrated that statistical learning produces both implicit and/or explicit knowledge depending on how the task is implemented (Batterink et al., 2015; Kim et al., 2009; Otsuka and Saiki, 2016). Perhaps the clearest support this comes from the contextual cuing paradigm where explicit judgments about the structure are dissociated from cuing behaviour since observers typically perform at chance on recognition tests after learning (Chun & Jiang, 1998, 2003), but see (Smyth and Shanks, 2008). Indeed, in our previous study, we observed that stimulation influenced contextual cuing but had no effect on recognition judgements. It is possible that a testing method where participants must make explicit judgements about structure may tap a different aspect of statistical knowledge than implicit cuing methods, and this may explain the differences in stimulation effects across the two tasks.

A second, and more parsimonious, explanation is that the recognition test lacked sensitivity to a learning process that evolves over time. The exposure–test format represents a persistent shortcoming in statistical learning research across the visual, motor and language domains which has been noted by other authors (Siegelman et al., 2016; Turk--Browne, 2014). When learning is only assessed once, at the end of the trials, it may miss critical aspects of learning that are dynamic, operate earlier in time, or are transient across the learning period. Indeed, Nydam et al. (2018) observed only transient disruption by tDCS, with cuing eventually reaching the same magnitude across all stimulation conditions. Therefore, it seems plausible that the offline recognition test may have missed any influence of tDCS on learning that occurred early during exposure, or may have reached an asymptote by the time learning was measured. Given our primary interest in the functional effects of visual statistical learning on behaviour, we decided to create an online task using the same shape-pair stimuli that was capable of measuring the potentially dynamic nature of tDCS effects of the formation of statistical learning.

6. Experiment 2

The second experiment set out to determine whether an online measure of learning would reveal causal involvement of cortical areas where an offline measure could not. To do this, we drew inspiration from the contextual cuing paradigm since it provides an online index of learning that is dissociable from practice effects and motor learning. The gap between cuing with spatial regularities and identity-based structure had already been bridged by existing variations of the paradigm (e.g., Chun and Jiang, 1999; Endo and Takeda, 2004). Thus, we married the shape-pair structure from the Fiser and Aslin paradigm with an incidental cuing task to create a new online measure of Visual Statistical Learning.

The new task retained the pair-structure from Experiment 1 by using the pair items as distractors in a series of visual arrays. A target item was added to create a visual search task which provided the online response-time measure across twelve blocks (collapsed into 3 epochs for analysis). Unbeknownst to participants there were two types of displays. In one condition, a given subset of distractors was associated with a given target location. The distractor set was defined by a unique combination of three base pairs (e.g., A, B, C) where the shapes had a fixed identity, but appeared in ever changing locations across the blocks. In a behavioural pilot, we observed a robust cuing benefit that appeared in epochs two and three. The response-time benefit was approximately 80 ms in magnitude, which was comparable to the spatial cuing effects observed in other work.

Using tDCS, we targeted the same the left posterior parietal region using either active (cathodal) stimulation or sham stimulation. The stimulation parameters were kept the same as in Experiment 1; namely, 15 min' duration at .7 mA. Our primary hypothesis the same as in Experiment 1, namely that learning in the active (cathodal) stimulation group would differ to learning in the sham group (non-directional hypothesis). This would indicate an effect of stimulation of learning. With our task now designed to be sensitive to the trajectory of learning over time, we also made a second prediction that was informed by the results of the previous contextual cuing study. We predicted the effect of tDCS would be different for an early phase of the task compared to a later phase.

We decided to drop the orbitofrontal control region and focus on having a double-blind-placebo-control design. Having only one active stimulation condition meant the experimenter could be blinded to the stimulation condition because there was no need to change cables (as would be needed with anodal and cathodal conditions) or to change the electrode montage (as would be needed with a control region). Given the potential biasing effects of experimenter instructions on the evolution of learning across time, this element of the design was crucial to assess our hypothesis regarding an early modulatory effect. Again, we had strong a priori predictions about the effect of cathodal currents based on the previous finding with contextual cuing.

7. Method

7.1. Participants

The design, hypotheses and analysis plan for Experiment 2 we logged prior to data collection [osf.io/7hqxe]. A total of 84 participants were recruited, however four were excluded prior to analysis because two failed to learn the appropriate key mappings and two experienced technical errors with the stimulator. This left a final sample of 80 participants (mean age = 20.43 years, 65% female, 36.25% glasses or contact use, mean Oldfield (1971) handedness score = 84.49%, mean Impedance = 16.95 kOhm).

7.2. Online visual statistical learning task

7.2.1. Stimuli

The stimuli were the same back shape-silhouettes arranged into six distractor-pairs and one target-pair (Fig. 3) selected from a pool of 24 shapes. Because the shapes had different surface areas, it was important to equate the size of shapes in the target pair, so that one shape was not more salient than the other, which could produce a pop-out effect when searching for the target. To address this, we sorted shapes based on total

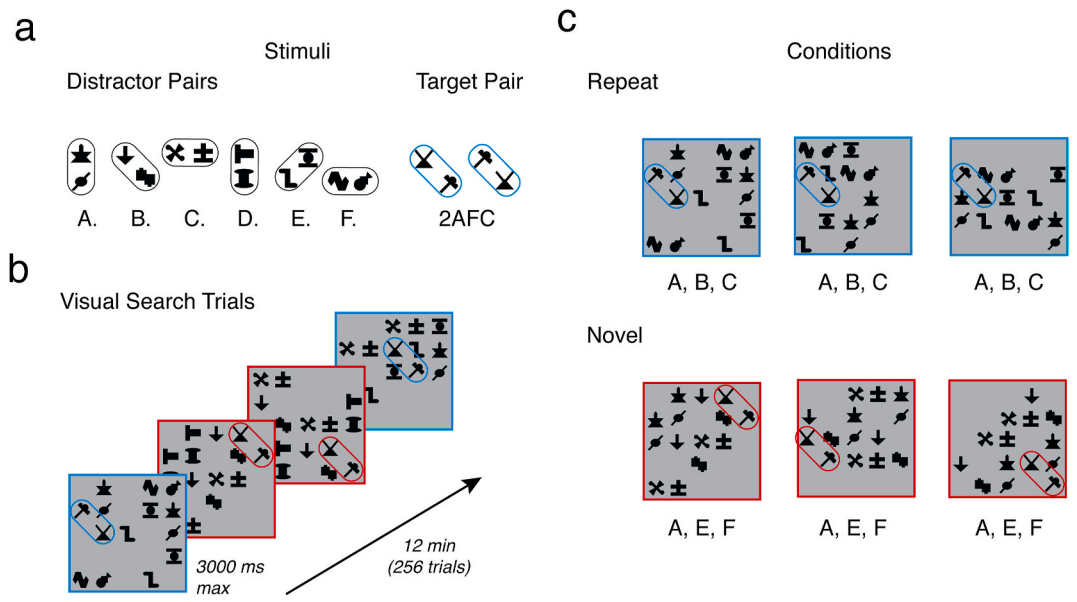

Fig. 3. The online Visual Statistical Learning paradigm used in Experiment 2. (a) The stimuli were the same as Experiment 1: six base pairs to serve as distractors (A, B, C, D, E, F) plus a seventh pair to serve as a target object. (b) Participants performed visual search to locate the target-pair (shown circled in red or blue) and respond to its orientation in a 2AFC manner. On each trial, the target pair appeared surrounded by three base pairs, each presented twice, to form a distractor subset that was defined by the item identities. (c) In the repeat condition, a given distractor subset (e.g., A, B, C) was consistently associated with a target location. In the novel condition, the association between subset (e.g., A, E, F) and target location was varied across blocks. Note that while each shape belonged to a single pair, each pair belonged to multiple subsets – meaning it was the specific combination of pairs in a distractor subset that was predictive (or non-predictive) of the target location. Red and blue circles and borders are for illustrative purposes and were not visible in the task. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

pixels before generating the target-pairs for each individual.

The task was to locate the target-pair, which was always on a diagonal, and report the arrangement of shapes being either "shape A above B" or "shape B above A". Responses were given using the 'z' and 'm' keys with index fingers on each hand. (Note an observer could also conceptualize the response as to report whether shape A was "above" or "below" shape B. Regardless, the task was to find two adjacent shapes among distractors and respond to a feature of that object by integrating across the two shapes. Participants practiced the response-mapping for 24 practice trials.

7.2.2. Target-Subset Association

While searching for the target pairs, observers encountered sets of distractors that were comprised of the base pairs used in the Fiser and Aslin paradigm from Experiment 1. To make search more difficult, each base-pair was shown twice, which required enlarging the grid from 3 × 3 cells to 5 × 5 cells. The six base-pairs were recombined to form eight subsets used in repeat trials and eight used in novel trials. Across the blocks, the shapes in repeat subsets appeared with fixed identities but in ever changing locations, and the subset cued the target pair location. The shapes in the novel subsets also repeated across blocks, but varied in relation to the target location. To control for target probability learning, we matched the number of target locations used in the repeat and novel conditions. It is worth noting that the repeat and novel conditions contained the same six base-pairs. It was the specific subset of pairs that defined a repeat or novel context. This meant that simply learning the pair structure alone was not sufficient to produce a cuing benefit.

Search trials began with a fixation cross for 500 ms (jittered between 100 and 500 ms), followed by the search display for 3000 ms, followed by a blank ITI for 500 ms. . If participants had not responded in the allotted time, a prompt screen appeared until response, Trials were arranged into 16 blocks of 16 trials (eight repeat and eight novel trials per block). Participants were encouraged to maintain accuracy above 85%. Every second block, the script would pause for a break and provide accuracy feedback. The apparatus was the same as Experiment 1: a 19″ CRT monitor (resolution 1024 × 768; refresh rate of 100 Hz) connected to an Apple iMac computer, with participants seated unrestrained approximately 63 cm from the screen.

7.3. Procedure

Participants attended a 1-h session where they completed a brief practice of 15 search trials before commencing the online statistical learning task with concurrent (online) stimulation that lasted 15 min. To enact the double-blind procedure, participants were randomly assigned to receive active (cathodal) or sham stimulation using a custom MATLAB script. It output a secret 5-digit code that the experimenter used to run the stimulator without knowing the condition allocations. After the stimulation, the electrodes were removed from the scalp, and participants completed the same recognition test as in Experiment 1. Finally, participants answered some open-ended questions which probed their awareness of the subset patterns and the stimulation type (sham control or active), then they were debriefed and paid AUS$20 for time and travel.

8. Results

8.1. Planned analyses

8.1.1. Stimulation effects on learning

Response times became increasingly faster in the repeat condition relative to the novel condition in both groups (Fig. 4, panel B). A 3-way ANOVA was computed on the epoch data (Fig. 4, panel A) with the factors: Trial Type (Repeat or Novel), Epoch (1–3), and Stimulation Group (Active or Sham). This revealed a main effect of Trial Type, $F_{1, 78} = 17.05$, $p < .001$, $\eta_p^2 = 0.18$, $BF_{10} = 21.293$, indicating an overall speed benefit for repeat arrays relative to novel arrays. There was also a main effect of Epoch, $F_{2, 156} = 67.10$, $p < .001$, $\eta_p^2 = 0.46$, $BF_{10} = 1.29e{+}42$, indicating a general speed improvement over time. Critically, the 3-way interaction - Trial Type × Epoch × Stimulation Group - was significant, F

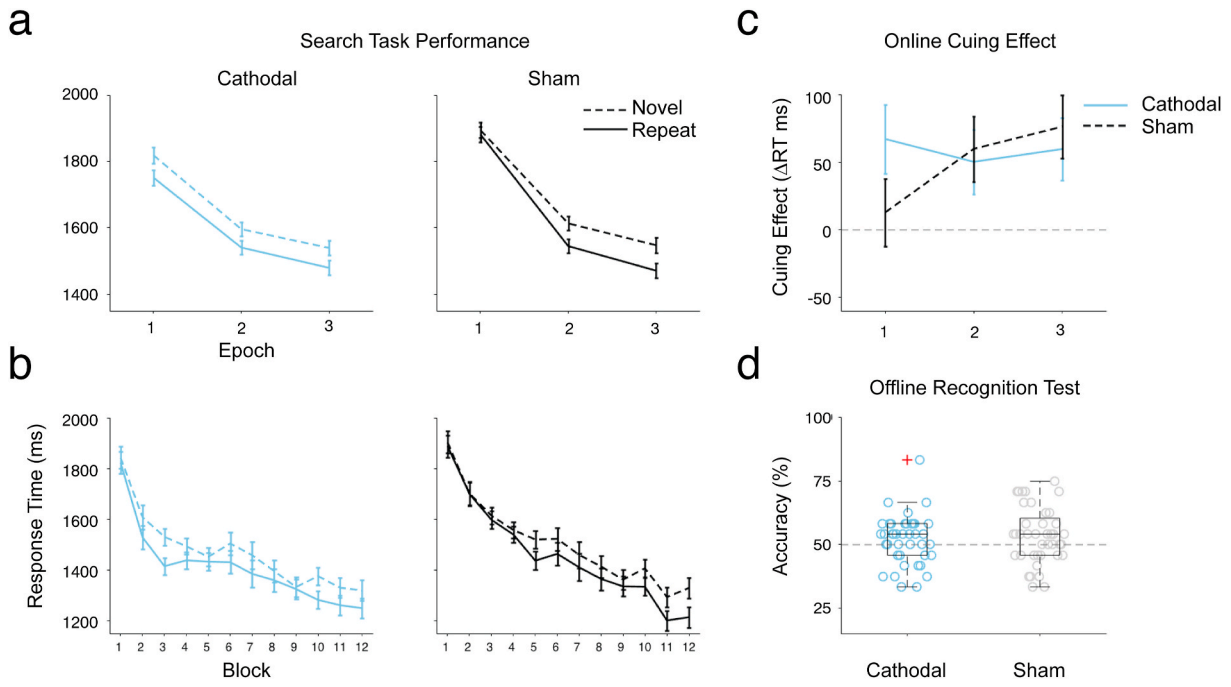

Fig. 4. Visual statistical learning effect in the two stimulation groups with the data shown across (a) epoch and (b) block. (c) The interaction between cuing magnitude and stimulation group across epochs. (d) Recognition of the base-pairs after stimulation was not affected by stimulation. Error bars indicate within-subjects standard error of the mean.

$_{1,\ 78}$ = 17.05, $p < .001$, $\eta_p^2 = 0.18$, $BF_{10} = 12.67$, in support of our prediction that stimulation affected identity-cuing (i.e., the Trial Type × Epoch effect) and the way it did so changed over the course of the task.

To follow-up the 3-way interaction, we ran planned ANOVAs to assess the nature of the cuing effect (Trial Type × Epoch) in each group separately. In the sham group, learning was characterized by a Trial Type × Epoch interaction, $F_{2,\ 78} = 5.023$, $p = .009$, $\eta_p^2 = 0.114$, indicating the cuing benefit emerged over time. There was also a main effect of Trial Type, $F_{1,\ 39} = 8.473$, $p = .006$, $\eta_p^2 = 0.178$, a main effect of Epoch, $F_{2,\ 78} = 33.19$, $p < .001$, $\eta_p^2 = 0.460$. Planned contrasts indicated how cuing was not present in Epoch 1, $t_{39} = -0.604$, $p = .549$, $BF_{10} = 0.291$, which showed a reliable null effect, but emerged over time and was robust in Epoch 2, $t_{39} = -3.531$, $p = .001$, $d^2 = -0.558$, $BF_{10} = 56.905$, and Epoch 3, $t_{39} = -3.459$, $p = .001$, $d^2 = -0.547$, $BF_{10} = 47.502$. The magnitude of the cuing benefit was 61 ms in Epoch 2 and 78 ms in Epoch 3, and the Bayes Factors indicated the data strongly favoured the cuing benefit over the null hypothesis.

Learning in the active stimulation group was characterized by a main effect of Trial Type, $F_{1,\ 39} = 8.595$, $p < .001$, $\eta_p^2 = 0.181$, along with a main effect of Epoch, $F_{2,\ 156} = 34.761$, $p < .001$, $\eta_p^2 = 0.471$, but no Trial Type × Epoch interaction, $F_{2,\ 78} = 0.202$, $p = .817$. This was because a cuing benefit was already robust in Epoch 1, $t_{39} = -2.571$, $p = .014$, $d^2 = -0.406$, $BF_{10} = 6.042$, and remained so for Epoch 2, $t_{39} = -2.726$, $p = .010$, $d^2 = -0.431$, $BF_{10} = 8.424$, and Epoch 3, $t_{39} = -2.545$, $p = .015$, $d^2 = -402$, $BF_{10} = 5.732$. The benefit was 65 ms, 50 ms and 58 ms across the epochs, and Bayes Factors favoured the alternate hypothesis over the null in all cases.

8.1.2. No baseline differences between groups

There were no differences between groups prior to learning; either in terms of the overall RT in block 1, $t_{78} = 0.342$, $p = .733$, or the cuing effect in block 1, $t_{78} = -0.0007$; $p = .994$, $BF_{10} = 0.234$. This confirms that the tDCS effect emerged over time with learning and cannot be explained by existing differences between the groups.

8.1.3. No effect of stimulation on overall RTs

When collapsing across Trial Type to look at overall RT changes, there was a general reduction across the blocks, $F_{2,\ 78} = 25.563$, $p < .001$, but no main effect of stimulation, $F_{1,\ 78} = 0.184$, $p = .669$, nor an interaction with stimulation, $F_{2,\ 78} = 0.381$, $p = .683$. This showed that tDCS did not cause a general change in procedural learning in the visual search task. Instead, the effect of stimulation was selective to statistical learning, being the difference between repeat and novel conditions over time. Consistent with this pattern, the overall RTs in Epoch 1 did not differ across the stimulation groups, $t_{78} = 0.342$; $p = .762$, only the cuing magnitude in Epoch 1was affected by the stimulation.

8.1.4. No effect of stimulation on accuracy

Accuracy was at ceiling, being consistently above 90%, and no individuals performed below the 75% exclusion cut-off. Analysis of the accuracy data revealed a main effect of Trial Type, $F_{1,\ 78} = 8.021$, $p = .006$, $\eta_p^2 = 0.093$, and Epoch, $F_{1,\ 78} = 5.670$, $p = .004$, $\eta_p^2 = 0.068$, to show that performance became both more accurate and faster for repeat subsets over time. The stimulation did not affect accuracy, as no other effects were significant (all other $ps > .215$). This confirmed there was no speed accuracy trade-off with cuing or with the stimulation effect.

8.1.5. No pair recognition after learning

As with Experiment 1, participants completed a recognition test on the pairs (Fig. 4, Panel D) but this time it was after the stimulation had ended. As expected, recognition did not differ between the groups, $t_{78} = -0.670$, $p = .505$, $BF_{10} = 0.271$, with the data favouring the null hypothesis over the alternate hypothesis. In the sham group, pair recognition significantly above chance, $t_{39} = 2.043$, $p = .049$. However, the data was in the unreliable range, $BF_{10} = 0.982$, and thus was likely to be spurious. Only 55% of individuals performed above chance in the sham group. In the Cathodal group recognition not significantly above chance, $t_{39} = 1.278$, $p = .210$. The data were inconclusive but trending toward support for the null hypothesis, $BF_{10} = 0.396$. In this group, only 52% of participants performed above chance. Permutation tests on recognition accuracy produced the same pattern of results. The mean deviation from chance (+3.54% > 2.92) was above the 95th percentile cutoff for the Sham group, but not for the Cathodal group (+1.98% < 2.6). These results show there was no reliable recognition of the pairs in Experiment

2.

8.2. Exploratory analysis

8.2.1. Early vs late learning effect

The results above showed that identity-cuing emerged earlier during active stimulation than during sham stimulation. To directly compare the early cuing effect in each group, we ran a 2-way ANOVA on cuing magnitude (novel RTs–repeat RTs) with factors Phase (Early and Late, i.e., Epoch 1 and Epoch 3) and Stimulation Group (Active and Sham). There was a significant Phase × Group interaction, $F_{1, 78} = 4.544$, $p = .036$, $\eta_p^2 = 0.055$, which provided a direct test to show that the difference in cuing magnitude between groups depended on the phase of learning. In Epoch 1, cuing magnitude was a 51 ms larger in the active group (65 ms ± 25.49) than in the sham group (14 ms ± 24.78). While this difference represented a meaningful advantage to search times, an independent samples *t*-test was not significant, $t_{78} = 1.422$, $p = .080$, $BF_{10} = 1.55$. The Bayes Factor was at least directionally consistent with the alternate hypothesis, however, with the data being only 1.5 times more likely under the alternate than under the null, the evidence was anecdotal at best, and suggests the need for more data to be collected in order to determine the nature of stimulation effects on learning.

To summarise, we observed that stimulation did affect visual statistical learning in a manner that changed over time (i.e., Trial Type × Epoch × Stimulation Group, $BF_{10} = 12.67$). The interaction appeared to be driven by an early benefit in the active stimulation group, that while functionally meaningful (i.e., a benefit of 50+ ms), the direct comparison was inconclusive.

9. General discussion

We investigated the effects of a non-invasive brain stimulation protocol on shaping the visuo-spatial statistical learning process. Across two experiments we used cathodal tDCS to modulate activity in the left posterior parietal cortex during exposure to visual structure. The visuospatial structure involved identity-based regularities, while controlling for location-based regularities. Based on the hypothesis that frontoparietal involvement reflects a general statistical learning process rather than a task-specific process, we predicted that the same tDCS protocol that affected learning spatial cues in contextual cuing would also modulate learning identity cues in this task. When stimulation was delivered during passive viewing, no effect on learning was detected (Experiment 1). When stimulation was delivered during the execution of a task, tDCS did have an effect on learning (Experiment 2). These results were consistent with the previous observation that cathodal tDCS altered the formation of statistical learning in a spatial contextual cuing task. Together, the findings provide support for the hypothesis that the activity in cortical regions, such as the left PPC, is causally involved in the visual statistical learning process.

Experiment 2 investigated whether the inconclusive findings from Experiment 1 related to the use of a one-shot recognition test that was not sensitive to learning across time. In line with this, we observed that tDCS *did* influence statistical learning when using an online task to track the learning process. The effect was not explained by pre-existing differences between the groups. Nor was it explained by a speed/accuracy trade-off, not a change in general task performance. Rather, tDCS specifically altered the *difference* between repeat and novel responses over time, which was our index of statistical processing. We concluded that administering tDCS over cortical regions can alter statistical learning of identity-based regularities.

A number of factors may have helped yield the positive result with our online task in Experiment 2. We discuss three plausible explanations. The first reason is that the tDCS-induced changes in neural activity interacted with task-based changes to alter the normal learning process. This account is consistent with previous work in the motor domain that observed similar interactions between excitability-altering stimulation and the degree of task-induced brain activity (e.g., Kuo, 2008; Stagg et al., 2011). For example, delivering anodal tDCS during a motor learning task enhanced learning, whereas offline stimulation reduced learning (Stagg et al., 2011). Perhaps more relevant is how delivering tDCS during a serial reaction time task altered learning, whereas delivering tDCS during a simple reaction time task did not affect learning (Kuo, 2008). The effects of task-engagement have also been reported with TMS, since theta-burst stimulation over the left DLPFC affected memory retrieval only when delivered during an active task condition, and not when delivered a during passive condition (Marin et al., 2018). This evidence supports the assertion that the degree of task engagement can modulate stimulation effects, in line with the broader activity-dependent hypothesis (i.e., Bikson and Rahman, 2013). Until now, similar regulatory mechanisms had not been documented outside the motor and primary sensory areas. The present work may suggest that similar regulatory mechanisms in higher-association areas also govern tDCS effects on the statistical learning process.

Nevertheless, it is not clear from the present results whether an early modulatory effect of tDCS may have been present with the passive viewing scenario in Experiment 1. Intermittent recognition tests have been used previously to show temporal changes in brain activity during passive statistical learning in the language domain (Karuza et al., 2013). Thus, a plausible alternative reason for the present result is that tDCS modulated the early formation of statistical learning, regardless of the active or passive nature of the task. A third possibility was that the involvement of associative mechanisms in the online task were responsible for the observed effect. The role of implicit prediction in cuing tasks might have meant that retrieval operations yielded the modulatory effect of tDCS in our online task. However, an effect of tDCS on retrieval would have likely manifested during the later phase, when the target-subset associations were more established, and not during the early phase as we observed. Given the known interactions between brain stimulation and endogenous brain activity (i.e., task-based activity), we prefer the explanation that an online task afforded the observation of an early modulatory effect. Future investigations should be conducted to determine the contribution of factors like passive viewing, visual search and predictive associations in modulating tDCS effects on statistical learning as well as behaviour more generally.

The ability to generalize findings about statistical learning across different tasks settings has been criticized by some in the broader literature. This was largely based on evidence showing that task aspects can change what is being learned about an underlying structure (Bays et al., 2016; Turk-Browne et al., 2005; Turk-Browne, Isola, Scholl and Treat, 2008a). Considering these criticisms, it was important to empirically examine the degree to which a given tDCS effect on statistical learning would generalize across task domains. The combined observations of a tDCS effect on behaviour when learning spatial regularities and identity-based (Aly and Turk-Browne, 2017) regularities strengthens the case for cortical involvement in a general statistical learning process. The causal evidence supports existing claims from the imaging literature that proposed higher-order cortical regions played an intervening role in the visual statistical learning process. While learning visuo-spatial regularities had consistently been associated with a network that included primary visual, parietal, frontal and medial temporal lobe structures, some studies had reported increased activity to regularities, while others reported decreased activity, and others focused on more dynamic connectivity patterns. The present findings are more in line with the suggestion that distinct patterns of neural activity, evoked by the task and stimuli, may be important for the formation of visual statistical learning effects on behaviour.

Stimulation affected identity-cuing in a time-varying manner that mirrored the early locus with spatial cuing observed previously (Nydam et al., 2018); albeit in the opposite direction (i.e., benefit vs. disruption). It is worth considering how a time selective or dynamic effect can arise when tDCS delivers a constant current throughout. Despite this fixed parameter, the impact of tDCS on excitability measures, such as motor

evoked potentials using TMS, is non-linear across time (Bonaiuto et al., 2016; Samani et al., 2019). So one explanation for the present result is that it reflect dynamic changes to excitability produced by tDCS. Yet tDCS-induced changes also reflect an interaction with task-based activity, and the encoding of statistical structure has been related to dynamic changes in task-evoked activity. For example, functional connectivity data across task domains had identified a dynamic hippocampal-parietal network during exposure to regularities (Karuza et al., 2017; Manelis and Reder, 2012). Compared to baseline, this network showed an early increase in connectivity, followed by a later decreased (Karuza et al., 2017). A similar network dynamic was reported in a visual-temporal learning paradigm (Turk-Browne et al., 2010), and may be a candidate for a domain-general mechanism (Batterink et al., 2019). The strongest evidence in support of this notion is how cuing behaviour was more strongly related to the early activity change than a later activity change (Manginelli et al., 2013). Given the totality of this evidence, we believe the dynamic nature of tDCS effects reflects dynamic changes in task-evoked activity over the learning period.

What do these early dynamics tell us about statistical learning more generally? There are two models of statistical learning that could explain such a dynamic trajectory. The two-stage model offers an explanation (Turk-Browne et al., 2005) based on the role of selective attention that is believed to decrease over time with learning. A more recent, but related, framework proposes that statistical learning can be decomposed into an early extraction stage and a later integration stage (Thiessen et al., 2013). Relating these two ideas back to the present work, the stimulation may have produced the most noticeable changes during an active stage that occurred early on. This proposal could be investigated in future work by commencing tDCS after different amounts of learning have taken place, to see if stimulation exerts a time-varying effect when delivered after the early stage has been completed.

Despite both contextual cuing and cuing with identity-structure showing an early effect, the direction of the effect was opposite. How could the same stimulation protocol impair spatial-cuing (i.e., Nydam et al., 2018) but facilitate identity-cuing (i.e., Experiment 2)? As a start, such variability is consistent with the broader tDCS literature. Cathodal currents may produce both facilitation and impairment in different contexts. Enhancement by cathodal tDCS was reported in the domains of visuospatial attention (Bolognini et al., 2010; Sparing et al., 2009), language acquisition (Floel et al., 2008; Meinzer et al., 2012), working memory (Fregni et al., 2005; Ohn et al., 2008; Zaehle et al., 2011), and recognition (Luo et al., 2017). Whereas, disruption by cathodal tDCS was reported for decision-making (Filmer et al., 2013). Adding to this complexity is the fact that tDCS-induced changes interact with task-generated activity to produce changes to measured output (Antal et al., 2007; Bortoletto et al., 2015). Meaning the task-based activity recruited by spatial-structure versus identity-structure may be distinct.

Another intriguing possibility relates to the modulatory role of attention in directing which statistics may be learned learning (Turk--Browne et al., 2005, Turk-Browne and Scholl, 2009). Behavioural work on contextual cuing has demonstrated that both spatial cues and identity cues can contribute to the incidental learning behaviour (Chun and Jiang, 1999; Endo and Takeda, 2004). However, when both cues were made available, there was a preference for learning the spatial cues (Endo and Takeda, 2004). The proposal that spatial cues may override identity cues under normal circumstances might explain how one could observe an opposing effect pf the same tDCS protocol across tasks as being based on the mechanism for spatial preference. If, under normal conditions, the system preferentially encodes spatial cues, then a cathodal tDCS protocol might yield a disruptive effect in a task where spatial cues are predictive (i.e., contextual cuing) but produce a benefit in a task where identity cues are predictive. Unlike the identity cuing task used previously, only identity cues were available in our task. Therefore, there is no way to know if there was a preference for one type of information over another. One way to test this empirically would be to use a task like Endo and Takeda (2004) to see if tDCS over the left PPC might reduce the spatial preference and bolster learning of identity cues, when both cue-types are available. The use of combined methods that are able to image the brain during, or close after, stimulation will be useful to inform better predictions about the directionality of stimulation effects. Broadly speaking, the difference in directionality we have observed embodies active and open debate concerning how to relate tDCS effects to measured behaviour in different tasks (Bestmann et al., 2015).

We observed converging evidence that a tDCS protocol using cathodal currents can influence the visuo-spatial statistical learning process across tasks. The use of a double-blind procedure in Experiment 2 meant we could be confident that the results were not due to systematic differences between active stimulation sessions and the sham sessions. That being said, we cannot yet make definitive conclusions (Ball et al., 2013) about the specificity of the parietal region without an active (Baker et al., 2004) control region. One alternative interpretation of the tDCS effect may be that anodal currents from the return electrode were producing the effect. We find this unlikely for two reasons. The mastoid is a popular and appropriate return electrode site used in many tDCS studies. This is because the electrode is positioned over a thick bony part of the skull where fewer currents may penetrate, and any that do are likely to be less focal than the current flow under the active electrode site. Our current flow modelling supported this notion, predicting the most concentrated area of current was located in the parietal lobe under the active/cathodal electrode. Therefore, we argue that changes in the cortex under the active electrode were responsible for the present effects.

We observed converging evidence that cortical activity plays an intervening role in the visuo-spatial statistical learning process across tasks. In order to understand the nature of this cortical mechanism it would be important to compare different types of stimulation (i.e., anodal and cathodal tDCS, tRNS or tACS) applied over different nodes in this distributed network. There is already evidence other types of stimulation can regulate implicit statistical learning in contextual cuing (Rosero Pahi et al., 2020). Specifically, theta-burst stimulation (TBS) over the left DLPFC was shown to improve spatial cuing compared to TBS over the vertex (Rosero Pahi et al., 2020). Improvements by TMS targeting the DLPFC have also been reported for unconscious perceptual memory (Lee et al., 2013). Meanwhile, long-term memory retrieval was disrupted by TBS over the DLPFC (Marin et al., 2018) and re-learning implicit cues was disrupted by rTMS over frontopolar cortex (Zinchenko et al., 2019). This mixed evidence fits with suggestions that the fronto-parietal network is recruited for memory-guided attention across a range of implicit and explicit task demands (Miller and Cohen, 2001; Pergolizzi and Chua, 2017; Wang et al., 2019; Ciaramelli and Moscovitch, 2020). While some have interpreted this evidence as support for the notion that cognitive control circuits in the DLPFC are not required for implicit behaviours; thereby explaining how “disrupting” these networks could facilitate learning (i.e., Lee et al., 2013; Rosero Pahi et al., 2020), we caution against interpreting our result as a “disruptive” effect. As stated, cathodal tDCS can have both facilitatory and inhibitory effects, and we did not measure neural activity changes directly. Furthermore, an account based on “disruption” of cognitive control regions cannot explain the disruptive effects of stimulation (Nydam et al., 2018; Marián et al., 2018). Instead, we interpret these results as being due to task-dependent activity in frontoparietal regions that can regulate the statistical learning process.

9.1. Conclusions

By modulating neural activity with tDCS during exposure to statistical regularities, we demonstrated that cortical brain activity is involved in the visual statistical learning process. In particular, these brain regions appear to be important for the way regularities are used to guide ongoing goal-directed behaviour. These empirical findings establish further causal evidence that the neural substrates of statistical learning likely involve brain regions beyond the sensory and medial

temporal lobe areas to include higher-level cortical regions within the frontal and parietal lobes. Most interestingly, the present findings converged on an early locus of cortical involvement that may relate to network dynamics in the parietal region that change with exposure to regularities. These findings add to theoretical understandings about how the brain produces incidental learning behaviour across different types of visual input and task settings.

Author statement

Abbey Nydam, Conceptualization, Investigation, Methodology, Software, Formal analysis, Data curation, Visualization, Writing - original draft. David Sewell, Supervision, Methodology, Writing - review & editing. Paul Dux, Conceptualization, Project administration, Methodology, Funding acquisition, Writing - review & editing.

Declaration of competing interest

The authors have no conflicts to declare, financial or otherwise.

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Appendix A. Supplementary data

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References

Abla, D., Katahira, K., Okanoya, K., 2008. On-line assessment of statistical learning by event-related potentials. J. Cognit. Neurosci 20 (6), 952–964. https://doi.org/10.1162/jocn.2008.20058.

Aly, M., Turk-Browne, N.B., 2016. Attention promotes episodic encoding by stabilizing hippocampal representations. Proc. Natl. Acad. Sci. Unit. States Am 113 (4), E420–E429. https://doi.org/10.1073/pnas.1518931113.

Aly, M., Turk-Browne, N.B., 2017. Flexible weighting of diverse inputs makes hippocampal function malleable. Neurosci. Lett 1–10. https://doi.org/10.1016/j.neulet.2017.05.063.

Antal, A, Terney, D, Poreisz, C, Paulus, W, 2007. Towards unravelling task-related modulations of neuroplastic changes induced in the human motor cortex. European Journal of Neuroscience 26, 2687–2691.

Arciuli, J., Torkildsen, J.V.K., Stevens, D.J., Simpson, I.C., 2014. Statistical learning under incidental versus intentional conditions. Feedforward and Feedback *5* (324), 199. https://doi.org/10.3389/fpsyg.2014.00747.

Baker, C.I., Olson, C.R., Behrmann, M., 2004. Role of attention and perceptual grouping in visual. Statistical Learning 15 (7), 460–466. https://doi.org/10.2307/40064133?ref=search-gateway:05521201c3c530d7b3d66487cbf0c128.

Ball, K., Lane, A.R., Smith, D.T., Ellison, A., 2013. Site-dependent effects of tDCS uncover dissociations in the communication network underlying the processing of visual search. Brain Stimulation 6 (6), 959–965. https://doi.org/10.1016/j.brs.2013.06.001.

Bassett, D, Mattar, M.G., 2017. A Network Neuroscience of Human Learning: Potential to Inform Quantitative Theories of Brain and Behavior. Trends in Cognitive Science 21 (4), 250–264. https://doi.org/10.1016/j.tics.2017.01.010.

Bassett, D, Yang, M, Wymbs, N.F, Grafton, S.T, 2015. Learning-induced autonomy of sensorimotor systems. Nature Neurosience 18 (5), 744–751. https://doi.org/10.1038/nn.3993.

Batsikadze, G., Moliadze, V., Paulus, W., Kuo, M.F., Nitsche, M.A., 2013. Partially non-linear stimulation intensity-dependent effects of direct current stimulation on motor cortex excitability in humans. J. Physiol 591 (7), 1987–2000.

Batterink, L.J., Paller, K.A., Reber, P.J., 2019. Understanding the neural bases of implicit and statistical learning. Topics in Cognitive Science 1 (1), 106–122. https://doi.org/10.1111/tops.12420.

Batterink, L.J., Reber, P.J., Neville, H.J., Paller, K.A., 2015. Implicit and explicit contributions to statistical learning. J. Mem. Lang 83, 62–78. https://doi.org/10.1016/j.jml.2015.04.004.

Bays, B.C., Turk-Browne, N.B., Seitz, A.R., 2016. Dissociable behavioural outcomes of visual statistical learning. Vis. Cognit 23 (9–10), 1072–1097. https://doi.org/10.1080/13506285.2016.1139647.

Bertolero, M, Basset, D, 2019. How the Mind Emerges from the Brain's Complex Networks. Scientific American 321 (1), 26–33.

Bestmann, S., de Berker, A.O., Bonaiuto, J., 2015. Understanding the behavioural consequences of noninvasive brain stimulation. Trends Cognit. Sci 19 (1), 13–20. https://doi.org/10.1016/j.tics.2014.10.003.

Biederman, I., Mezzanotte, R.J., Rabinowitz, J.C., 1982. Scene perception: detecting and judging objects undergoing relational violations. Cognit. Psychol 14 (2), 143–177. https://doi.org/10.1016/0010-0285(82)90007-X.

Bikson, M., Rahman, A., 2013. Origins of specificity during tDCS: anatomical, activity-selective, and input-bias mechanisms. Front. Hum. Neurosci 7, 688. https://doi.org/10.3389/fnhum.2013.00688.

Bolognini, N, Olgiati, E, Rossetti, A, Maravita, A, 2010. Enhancing multisensory spatial orienting by brain polarization of the parietal cortex. European Journal of Neuroscience.

Bonaiuto, J.J., de Berker, A., Bestmann, S., 2016. Changes in Attractor Dynamics Predict Altered Perceptual Decision Making with Dorsolateral Prefrontal tDCS. https://doi.org/10.1101/036905.

Bortoletto, M., Pellicciari, M.C., Rodella, C., Miniussi, C., 2015. The interaction with task-induced activity is more important than polarization: a tDCS study. Brain stimulation 8 (2), 269–276.

Chun, M.M., Jiang, Y., 1998. Contextual cueing: implicit learning and memory of visual context guides spatial attention. Cognit. Psychol 36 (1), 28–71. https://doi.org/10.1006/cogp.1998.0681.

Chun, M.M., Jiang, Y., 1999. Top-down attentional guidance based on implicit learning of visual covariation. Psychological Science 10 (4), 360–365. https://doi.org/10.1111/1467-9280.00168.

Chun, M.M., Jiang, Y., 2003. Implicit, long-term spatial contextual memory. J. Exp. Psychol. Learn. Mem. Cognit 29 (2), 224–234. https://doi.org/10.1037/0278-7393.29.2.224.

Chun, M.M., Turk-Browne, N.B., 2008. Associative learning mechanisms in vision. In: Visual Memory. Oxford University Press, pp. 209–246. https://doi.org/10.1093/acprof:oso/9780195305487.003.0007.

Ciaramelli, E., Moscovitch, M., 2020. The space for memory in posterior parietal cortex: Re-analyses of bottom-up attention data. Neuropsychologia, 107551.

Conway, C.M., Christiansen, M.H., 2005. Modality-constrained statistical learning of tactile, visual, and auditory sequences. J. Exp. Psychol. Learn. Mem. Cognit 31 (1), 24–39. https://doi.org/10.1037/0278-7393.31.1.24.

Conway, C.M., Christiansen, M.H., 2006. Statistical Learning within and between Modalities, vols. 1–8.

Conway, C.M., Goldstone, R.L., Christiansen, M.H., 2007. Perceptual constraints on visual statistical learning of multielement scenes. In: McNamara, D.S., Trafton, J.G. (Eds.), Proceedings of the 29th Annual Meeting of the Cognitive Science Society. Cognitive Science Society, Austin, TX, pp. 185–190. https://doi.org/10.1037/e527352012-865.

Covington, N.V., Brown-Schmidt, S., Duff, M.C., 2018. The necessity of the Hippocampus for statistical learning. J. Cognit. Neurosci 20, 1–20. https://doi.org/10.1162/jocn_a_01228.

Cunillera, T., Camara, E., Toro, J.M., Marco-Pallares, J., Sebastian-Galles, N., Ortiz, H., Rodrıguez- Fornells, A., 2009. Time course and functional neuroanatomy of speech segmentation in adults. Neuroimage 48 (3), 541–553.

Dayan, E., Censor, N., Buch, E.R., Sandrini, M., Cohen, L.G., 2013. Noninvasive brain stimulation: from physiology to network dynamics and back. Nat. Neurosci 16 (7), 838–844. https://doi.org/10.1038/nn.3422.

Dosenbach, N.U.F, Fair, D.A., Miezin, F.M., Cohen, A.L., Wenger, K.K., et, al, 2007. Distinct brain networks for adaptive and stable task control in humans. Proceedings of the National Academy of Sciences J 104 (26), 11073–11078. https://doi.org/10.1073/pnas.0704320104.

Duncan, J, 2010. The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. Trends in Cognitive Science 14 (4). https://doi.org/10.1016/j.tics.2010.01.004. Epub 2010 Feb 18. PMID: 20171926.

Duncan, J, Owen, A.M, 2000. Common regions of the human frontal lobe recruited by diverse cognitive demands. Trends in Neurosciences 23 (10), 475–483. https://doi.org/10.1016/S0166-2236(00)01633-7.

Endo, N., Takeda, Y., 2004. Selective learning of spatial configuration and object identity in visual search. Percept. Psychophys 66 (2), 293–302.

Fedorenko, E., Duncan, J., Kanwisher, N., 2012. Language-selective and domain-general regions lie side by side within Broca's area. Curr. Biol 22 (21), 2059–2062.

Filmer, H.L., Dux, P.E., Mattingley, J.B., 2014. Applications of transcranial direct current stimulation for understanding brain function. Trends Neurosci 37 (12), 742–753. https://doi.org/10.1016/j.tins.2014.08.003.

Filmer, H.L., Lyons, M., Mattingley, J.B., Dux, P.E., 2017a. Anodal tDCS applied during multitasking training leads to transferable performance gains. Sci. Rep 1–11. https://doi.org/10.1038/s41598-017-13075-y.

Filmer, H.L., Mattingley, J.B., Marois, R., Dux, P.E., 2013. Disrupting prefrontal cortex prevents performance gains from sensory-motor training. J. Neurosci 33 (47), 18654–18660. https://doi.org/10.1523/JNEUROSCI.2019-13.2013.

Filmer, H.L., Varghese, E., Hawkins, G.E., Mattingley, J.B., Dux, P.E., 2017b. Improvements in attention and decision-making following combined behavioral training and brain stimulation. Cerebr. Cortex 27 (7), 3675–3682. https://doi.org/10.1093/cercor/bhw189.

Fiser, J., Aslin, R.N., 2001. Unsupervised statistical learning of higher-order spatial structures from visual scenes. Psychol. Sci 12 (6), 499–504. https://doi.org/10.1111/1467-9280.00392.

Fiser, J., Aslin, R.N., 2002a. Statistical learning of higher-order temporal structure from visual shape sequences. J. Exp. Psychol. Learn. Mem. Cognit 28 (3), 458–467. https://doi.org/10.1037/0278-7393.28.3.458.

Fiser, J., Aslin, R.N., 2002b. Statistical learning of higher-order temporal structure from visual shape sequences. J. Exp. Psychol. Learn. Mem. Cognit 28 (3), 458–467. https://doi.org/10.1037//0278-7393.28.3.458.
Fiser, J., Aslin, R.N., 2005. Encoding multielement scenes: statistical learning of visual feature hierarchies. J. Exp. Psychol. Gen 134 (4), 521–537. https://doi.org/10.1037/0096-3445.134.4.521.
Fiser, J., Lengyel, G., 2019. A common probabilistic framework for perceptual and statistical learning. Curr. Opin. Neurobiol 58, 218–228.
Floel, A, Rosser, N, Michka, O, Knecht, S, Breitenstein, C, 2008. Noninvasive Brain Stimulation Improves Language Learning. Journal of Cognitive Neuroscience 20 (8), 1415–1422.
Fregni, F, Boggio, P.S., Nitsche, M, et, al, 2005. Anodal transcranial direct current stimulation of prefrontal cortex enhances working memory. Experimental Brain Research 166 (1), 23–30. https://doi.org/10.1007/s00221-005-2334-6. Epub 2005 Jul 6. PMID: 15999258.
Friedman, A., 1979. Framing pictures: the role of knowledge in automatized encoding and memory for gist. J. Exp. Psychol. Gen 108 (3), 316–355. https://doi.org/10.1037/0096-3445.108.3.316.
Frost, R., Armstrong, B.C., Siegelman, N., Christiansen, M.H., 2015. Domain generality versus modality specificity: the paradox of statistical learning. Trends Cognit. Sci 19 (3), 117–125. https://doi.org/10.1016/j.tics.2014.12.010.
Gheysen, F., Van Opstal, F., Roggeman, C., Van Waelvelde, H., Fias, W., 2010. Hippocampal contribution to early and later stages of implicit motor sequence learning. Exp. Brain Res 202 (4), 795–807. https://doi.org/10.1007/s00221-010-2186-6.
Giesbrecht, B., Sy, J.L., Guerin, S.A., 2013. Both memory and attention systems contribute to visual search for targets cued by implicitly learned context. Vis. Res 85, 80–89. https://doi.org/10.1016/j.visres.2012.10.006.
Goujon, A., Didierjean, A., Thorpe, S., 2015. Investigating implicit statistical learning mechanisms through contextual cueing. Trends Cognit. Sci 19 (9), 524–533. https://doi.org/10.1016/j.tics.2015.07.009.
Hall, M.G., Naughtin, C.K., Mattingley, J.B., Dux, P.E., 2018. Distributed and opposing effects of incidental learning in the human brain. Neuroimage 173, 351–360. https://doi.org/10.1016/j.neuroimage.2018.02.068.
Henderson, J.M., Weeks, P.A., Hollingworth, A., 1999. The effects of semantic consistency on eye movements during complex scene viewing. J. Exp. Psychol. Hum. Percept. Perform 25 (1), 210–228. https://doi.org/10.1037/0096-1523.25.1.210.
Karuza, E.A., Emberson, L.L., Roser, M.E., Cole, D., Aslin, R.N., Fiser, J., 2017. Neural signatures of spatial statistical learning: characterizing the extraction of structure from complex visual scenes. J. Cognit. Neurosci 29 (12), 1963–1976. https://doi.org/10.1162/jocn_a_01182.
Karuza, E.A., Newport, E.L., Aslin, R.N., Starling, S.J., Tivarus, M.E., Bavelier, D., 2013. Neural correlates of statistical learning in a word segmentation task: an fMRI study. Brain Lang 127, 46–54.
Kim, R., Seitz, A., Feenstra, H., Shams, L., 2009. Testing assumptions of statistical learning: is it long-term and implicit? Neurosci. Lett 461 (2), 145–149. https://doi.org/10.1016/j.neulet.2009.06.030.
Kirkham, N.Z., Slemmer, J.A., Johnson, S.P., 2002. Visual statistical learning in infancy: evidence for a domain general learning mechanism. Cognition 83 (2), B35–B42. https://doi.org/10.1016/S0010-0277(02)00004-5.
Kuo, M.F., et al., 2008. Limited impact of homeostatic plasticity on motor learning in humans. Neuropsychologia. https://doi.org/10.1016/j.neuropsychologia.2008.02.023.
Lee, T.G., Blumenfeld, R.S., d'Esposito, M., 2013. Disruption of dorsolateral but not ventrolateral prefrontal cortex improves unconscious perceptual memories. J. Neurosci 33 (32), 13233–13237.
Luo, J, Hang, L, Zheng, H, Chen, S, Huang, D, 2017. Modulating the activity of the dorsolateral prefrontal cortex by tDCS alters distributive decisions behind the veil of ignorance via risk preference. Behavioural Brain Research 328.
Luo, Y., Zhao, J., 2017. Learning induced illusions: statistical regularities create false memories. J. Vis 17 (10), 503. https://doi.org/10.1167/17.10.503.
Manelis, A., Reder, L.M., 2012. Procedural learning and associative memory mechanisms contribute to contextual cueing: evidence from fMRI and eye-tracking. Learn. Mem 19 (11), 527–534. https://doi.org/10.1101/lm.025973.112.
Manginelli, A.A., Baumgartner, F., Pollmann, S., 2013. Dorsal and ventral working memory-related brain areas support distinct processes in contextual cueing. Neuroimage 67, 363–374. https://doi.org/10.1016/j.neuroimage.2012.11.025.
Marián, M., Szőllősi, Á., Racsmány, M., 2018. Anodal transcranial direct current stimulation of the right dorsolateral prefrontal cortex impairs long-term retention of reencountered memories. Cortex 108, 80–91. https://doi.org/10.1016/j.cortex.2018.07.012.
Marin, B.M., VanHaerents, S.A., Voss, J.L., Bridge, D.J., 2018. Prefrontal theta-burst stimulation disrupts the organizing influence of active short-term retrieval on episodic memory. Eneuro.
Meinzer, M, Antonenko, D, Lindenberg, R, Hetzer, S, et, al, 2012. Electrical Brain Stimulation Improves Cognitive Performance by Modulating Functional Connectivity and Task-Specific Activation. Journal of Neuroscience 32 (5), 1859–1866. https://doi.org/10.1523/JNEUROSCI.4812-11.2012.
Miller, E.K., Cohen, J.D., 2001. An integrative theory of prefrontal cortex function. Annu. Rev. Neurosci 24 (1), 167–202.
Nitsche, M.A., Paulus, W., 2000. Excitability changes induced in the human motor cortex by weak transcranial direct current stimulation. J. Physiol 527 (3), 633–639. https://doi.org/10.1111/j.1469-7793.2000.t01-1-00633.x.
Nitsche, M.A., Cohen, L.G., Wassermann, E.M., Priori, A., Lang, N., Antal, A., et al., 2008. Transcranial direct current stimulation: state of the art 2008. Brain Stimulation 1 (3), 206–223. https://doi.org/10.1016/j.brs.2008.06.004.
Nitsche, M.A., Liebetanz, D., Lang, N., Antal, A., Tergau, F., Paulus, W., 2003a. Safety criteria for transcranial direct current stimulation (tDCS) in humans. Clin. Neurophysiol 114 (11), 2220–2222. https://doi.org/10.1016/S1388-2457(03)00235-9.
Nitsche, M.A., Schauenburg, A., Lang, N., Liebetanz, D., Exner, C., Paulus, W., Tergau, F., 2003b. Facilitation of implicit motor learning by weak transcranial direct current stimulation of the primary motor cortex in the human. J. Cognit. Neurosci 15 (4), 619–626. https://doi.org/10.1162/089892903321662994.
Nydam, A.S., Sewell, D.K., Dux, P.E., 2018. Cathodal electrical stimulation of frontoparietal cortex disrupts statistical learning of visual configural information. Cortex 99, 187–199. https://doi.org/10.1016/j.cortex.2017.11.008.
Ohn, S.H., Park, C, Yoo, W, Ko, M, et, al, 2008. Time-dependent e¡ect of transcranial direct current stimulation on the enhancement of working memory. Cognitive Neuroscience and Neuropsychology 19 (1).
Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9 (1), 97–113. https://doi.org/10.1016/0028-3932(71)90067-4.
Orbán, G., Fiser, J., Aslin, R.N., Lengyel, M., 2008. Bayesian learning of visual chunks by human observers. Proc. Natl. Acad. Sci. U. S. A 105 (7), 2745–2750. https://doi.org/10.2307/25451537?refreqid=search-gateway:3dc862be2ff965b4f01372f95f88b014.
Otsuka, S., Saiki, J., 2016. Gift from statistical learning: visual statistical learning enhances memory for sequence elements and impairs memory for items that disrupt regularities. Cognition 147 (C), 113–126. https://doi.org/10.1016/j.cognition.2015.11.004.
Pergolizzi, D., Chua, E.F., 2017. Increased contextual cue utilization with tDCS over the prefrontal cortex during a recognition task. Brain Res 1655, 1–9. https://doi.org/10.1016/j.brainres.2016.11.008.
Perruchet, P., Pacton, S., 2006. Implicit learning and statistical learning: one phenomenon, two approaches. Trends Cognit. Sci 10 (5), 233–238. https://doi.org/10.1016/j.tics.2006.03.006.
Pollmann, S., 2012. Anterior prefrontal contributions to implicit attention control. Brain Sci 2 (4), 254–266. https://doi.org/10.3390/brainsci2020254.
Pollmann, S., Manginelli, A.A., 2010. Repeated contextual search cues lead to reduced BOLD-onset times in early visual and left inferior frontal cortex. Open Neuroimaging J 4, 9–15. https://doi.org/10.2174/1874440001004010009.
Reis, J., Schambra, H.M., Cohen, L.G., Buch, E.R., Fritsch, B., Zarahn, E., et al., 2009. Noninvasive cortical stimulation enhances motor skill acquisition over multiple days through an effect on consolidation. Proc. Natl. Acad. Sci. Unit. States Am 106 (5), 1590–1595. https://doi.org/10.1073/pnas.0805413106.
Roser, M.E., Aslin, R.N., McKenzie, R., Zahra, D., Fiser, J., 2015. Enhanced visual statistical learning in adults with autism. Neuropsychology 29 (2), 163–172. https://doi.org/10.1037/neu0000137.
Rosero Pahi, M., Cavalli, J., Nees, F., Flor, H., Andoh, J., 2020. Disruption of the prefrontal cortex improves implicit contextual memory-guided attention: combined behavioral and electrophysiological evidence. Cerebr. Cortex 30 (1), 20–30.
Ruhnau, P., Rufener, K.S., Heinze, H.J., Zaehle, T., 2018. Sailing in a sea of disbelief: in vivo measurements of transcranial electric stimulation in human subcortical structures. Brain Stimulation 11 (1), 241–243. https://doi.org/10.1016/j.brs.2017.09.015.
Samani, M.M., Agboada, D., Jamil, A., Kuo, M.F., Nitsche, M.A., 2019. Titrating the neuroplastic effects of cathodal transcranial direct current stimulation (tDCS) over the primary motor cortex. Cortex 119, 350–361.
Schapiro, A.C., Gregory, E., Landau, B., McCloskey, M., Turk-Browne, N.B., 2014. The necessity of the medial temporal lobe for statistical learning. J. Cognit. Neurosci 26 (8), 1736–1747. https://doi.org/10.1162/jocn_a_00578.
Schapiro, A.C., Kustner, L.V., Turk-Browne, N.B., 2012. Shaping of object representations in the human medial temporal lobe based on temporal regularities. Curr. Biol 22 (17), 1622–1627. https://doi.org/10.1016/j.cub.2012.06.056.
Schapiro, A.C., Turk-Browne, N.B., Norman, K.A., Botvinick, M.M., 2016. Statistical learning of temporal community structure in the hippocampus. Hippocampus 26 (1), 3–8. https://doi.org/10.1002/hipo.22523.
Siegelman, N., Bogaerts, L., Frost, R., 2017. Measuring individual differences in statistical learning: current pitfalls and possible solutions, pp. 1–15 http://doi.org/10.3758/s13428-016-0719-z.
Siegelman, N., Bogaerts, L., Christiansen, M.H., Frost, R., 2016. Towards a theory of individual differences in statistical learning. Phil. Trans. R. Soc. B 372 (1711), 20160059. https://doi.org/10.1098/rstb.2016.0059.
Smyth, A.C., Shanks, D.R., 2008. Awareness in contextual cuing with extended and concurrent explicit tests. Mem. Cognit 36 (2), 403–415. https://doi.org/10.3758/MC.36.2.403.
Sparing, R, Thimm, M, Hesse, M.D., Küst, J, Karbe, H, Fink, G.R., 2009. Bidirectional alterations of interhemispheric parietal balance by non-invasive cortical stimulation. Brain 132, 3011–3020. https://doi.org/10.1093/brain/awp154, pmid:19528092.
Stagg, C.J., Jayaram, G, Pastor, D, Kincses, Z.T., Matthews, P.M., Johansen-Berga, H, et al., 2011. Polarity and timing-dependent effects of transcranial direct current stimulation in explicit motor learning. Neuropsychologia 49 (5), 800–804.
Thiessen, E.D., Kronstein, A.T., Hufnagle, D.G., 2013. The extraction and integration framework: a two-process account of statistical learning. Psychol. Bull 139 (4), 792–814. https://doi.org/10.1037/a0030801.
Turk-Browne, N.B., 2014. Statistical learning and its consequences. In: Stoltenberg, S.F. (Ed.), Genes and the Motivation to Use Substances. Springer New York, New York, NY, pp. 117–146. https://doi.org/10.1007/978-1-4614-4794-8_6.
Turk-Browne, N.B., Scholl, B.J., 2009. Flexible visual statistical learning: transfer across space and time. J. Exp. Psychol. Hum. Percept. Perform 35 (1), 195–202. https://doi.org/10.1037/0096-1523.35.1.195.

Turk-Browne, N.B., Isola, P.J., Scholl, B.J., Treat, T.A., 2008a. Multidimensional visual statistical learning. J. Exp. Psychol. Learn. Mem. Cognit 34 (2), 399–407. https://doi.org/10.1037/0278-7393.34.2.399.

Turk-Browne, N.B., Johnson, M.K., Chun, M.M., Scholl, B.J., 2008b. Neural evidence of statistical learning: incidental detection and anticipation of regularities. J. Vis 8 (6), 695. https://doi.org/10.1167/8.6.695.

Turk-Browne, N.B., Jungé, J.A., Scholl, B.J., 2005. The automaticity of visual statistical learning. J. Exp. Psychol. Gen 134 (4), 552–564. https://doi.org/10.1037/0096-3445.134.4.552.

Turk-Browne, N.B., Scholl, B.J., Johnson, M.K., Chun, M.M., 2010. Implicit perceptual anticipation triggered by statistical learning. J. Neurosci. : the Official Journal of the Society for Neuroscience 30 (33), 11177–11187. https://doi.org/10.1523/JNEUROSCI.0858-10.2010.

Wagenmakers, E.-J., Love, J., Marsman, M., Jamil, T., Ly, A., Verhagen, J., et al., 2017. Bayesian inference for psychology. Part II: example applications with JASP. Psychon. Bull. Rev 25 (1), 58–76. https://doi.org/10.3758/s13423-017-1323-7.

Wang, L., Amalric, M., Fang, W., Jiang, X., Pallier, C., Figueira, S., et al., 2019. Representation of spatial sequences using nested rules in human prefrontal cortex. Neuroimage 186, 245–255. https://doi.org/10.1016/j.neuroimage.2018.10.061.

Zaehle, T, Sandmann, P, Thorne, J.D., et, al., 2011. Transcranial direct current stimulation of the prefrontal cortex modulates working memory performance: combined behavioural and electrophysiological evidence. BMC Neurosci 12 (2). https://doi.org/10.1186/1471-2202-12-2.

Zhao, J., Ngo, N., McKendrick, R., Turk-Browne, N.B., 2011. Mutual interference between statistical summary perception and statistical learning. Psychol. Sci 22 (9), 1212–1219. https://doi.org/10.1177/0956797611419304.

Zinchenko, A., Conci, M., Taylor, P.C.J., Müller, H.J., Geyer, T., 2019. Taking attention out of context: frontopolar transcranial magnetic stimulation abolishes the formation of new context memories in visual search. J. Cognit. Neurosci 31 (3), 442–452. https://doi.org/10.1162/jocn_a_01358.