Neuropsychologia 51 (2013) 1234–1239

Contents lists available at SciVerse ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

# Anodal tDCS to V1 blocks visual perceptual learning consolidation

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ARTICLE INFO

*Article history:*
Received 1 February 2013
Received in revised form
15 March 2013
Accepted 22 March 2013
Available online 2 April 2013

*Keywords:*
Transcranial direct current stimulation
Visual perception
Perceptual learning
External modulation of visual cortex
Contrast enhancement
Consolidation
Visual learning
Anodal tDCS

ABSTRACT

This study examined the effects of visual cortex transcranial direct current stimulation (tDCS) on visual processing and learning. Participants performed a contrast detection task on two consecutive days. Each session consisted of a baseline measurement followed by measurements made during active or sham stimulation. On the first day, one group received anodal stimulation to primary visual cortex (V1), while another received cathodal stimulation. Stimulation polarity was reversed for these groups on the second day. The third (control) group of subjects received sham stimulation on both days. No improvements or decrements in contrast sensitivity relative to the same-day baseline were observed during real tDCS, nor was any within-session learning trend observed. However, task performance improved significantly from Day 1 to Day 2 for the participants who received cathodal tDCS on Day 1 and for the sham group. No such improvement was found for the participants who received anodal stimulation on Day 1, indicating that anodal tDCS blocked overnight consolidation of visual learning, perhaps through engagement of inhibitory homeostatic plasticity mechanisms or alteration of the signal-to-noise ratio within stimulated cortex. These results show that applying tDCS to the visual cortex can modify consolidation of visual learning.



## 1. Introduction

Transcranial direct current stimulation (tDCS) is a noninvasive method for modulating cortical activity by which a direct electrical current is passed through two or more electrodes placed on the scalp over target cortical areas (Nitsche & Paulus, 2000). It is assumed that tDCS can produce excitability changes in the underlying cortex. Anodal stimulation (a-tDCS) is thought to cause depolarization of neuronal membranes directly under the electrode, resulting in increased excitability and, consequently, increased baseline firing rates. Cathodal stimulation (c-tDCS), conversely, is typically thought to have the opposite effect, hyperpolarizing membranes and thus causing decreases in excitability and spontaneous firing (Antal & Paulus, 2008). Measures of neuronal activity (EEG, Antal, Kincses, Nitsche, Bartfai, & Paulus, 2004; fMRI, Baudewig, Nitsche, & Paulus, 2001) have confirmed the modulatory effect of tDCS on the human cortex, which can last for up to 90 min in the human motor cortex (Nitsche & Paulus, 2001). For example, tDCS of primary visual cortex (V1) can modulate the amplitude of the N70 component of the visual evoked potential in response to low-contrast visual stimuli in a polarity specific manner (Antal et al., 2004). However, it is important to note that these effects are not ubiquitous, and the nature of the effect can depend on electrical current intensity, neuron type, cortical area, and spatial configuration of electrodes. For instance, a-tDCS to occipital areas reduces the amplitude of the P100, whereas c-tDCS increases its amplitude (Accornero, Li Voti, La Riccia, & Gregori, 2007). Further, c-tDCS over MT+ (area V5) has recently been shown to result in *increased* BOLD signal in comparison to sham stimulation (Antal, Kovács, Chaieb, Cziraki, & Paulus, 2012)—a-tDCS was not reported in this study. It has also been suggested that a-tDCS may reduce GABA concentration in motor cortex (Boros, Poreisz, Münchau, Paulus, & Nitsche, 2008; Stagg et al., 2009; Stagg & Nitsche, 2011) and visual cortex (Spiegel, Hansen, Byblow, & Thompson, 2012). GABA plays an important role in differentiating stimulus-evoked activity from background spontaneous firing (Leventhal, Wang, Pu, Zhou, & Ma, 2003) and, consequently, affects the quality of a stimulus-dependent signal. There is also evidence that tDCS can engage homeostatic regulatory mechanisms that control and stabilize excitability levels (Lang et al., 2007; Siebner et al., 2004).

"Typical" polarity-specific behavioral effects of tDCS have been documented in humans (Nitsche & Paulus, 2000). Within the visual domain, it has been shown that phosphene thresholds are

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http://dx.doi.org/10.1016/j.neuropsychologia.2013.03.013

significantly reduced as a result of occipital a-tDCS, but raised through c-tDCS (Antal, Kincses, Nitsche, & Paulus, 2003a, b). Additionally, in comparison to baseline performance on a previous day, c-tDCS to primary visual cortex (V1) was shown to decrease contrast sensitivity (i.e., raise detection thresholds), while a-tDCS was shown to have no effect on detection of gratings—probably due to a ceiling effect (Antal, Nitsche, & Paulus, 2001).

The above studies, investigating the effect of tDCS on visual perception, all measure performance during or after stimulation relative to baseline performance measured on a separate day, prior to stimulation days. To our knowledge, only one study has assessed the perceptual effect of tDCS in comparison to baselines taken on the same day as stimulation, which allows for an assessment of any task learning effects. This study (Kraft et al., 2010) investigated the effects of anodal, cathodal, and sham tDCS on threshold perimetry, and found that thresholds were reduced in central locations as a result of a-tDCS in comparison to same-day baseline performance. No changes resulted from cathodal or sham stimulation.

### 1.1. tDCS and learning

Several studies have examined the role of tDCS on motor learning. For example, it has been shown that a-tDCS to primary motor cortex (M1) increased within-session learning on a sequence learning motor task, while cathodal and sham tDCS had no effect, nor did stimulation of premotor or prefrontal areas (Nitsche et al., 2003). Anodal tDCS to M1 has also been demonstrated to result in enhanced formation and retention of motor memories in comparison to sham stimulation, assessed through performance on a learned thumb movement task (Galea & Celnik, 2009); c-tDCS was not assessed in this study. Similarly, in a sequence learning motor task, a-tDCS was associated with faster learning and c-tDCS with slower learning, when applied during the learning phase of the task (Stagg et al., 2011).

In contrast to the large number of studies of tDCS and motor learning, there is a relative dearth of learning and consolidation studies within the perceptual domain. However, one of the few studies in this area has demonstrated that external modulation of cortical excitability using high-frequency transcranial random noise stimulation (tRNS) can affect visual perceptual learning. An alternating current of high random frequencies (100–640 Hz) applied to the occipital cortex led to significantly greater benefits in within-session learning of an orientation discrimination task than low-frequency tRNS (.1–100 Hz) or anodal tDCS. In fact, a-tDCS did not produce statistically significant learning improvements over baseline and sham conditions (Fertonani, Pirulli, & Miniussi, 2011). A follow-up study replicated the facilitatory effect of concurrent high-frequency tRNS on performance, but additionally demonstrated that a-tDCS can produce similar improvements when applied *before* task execution (Pirulli, Fertonani, & Miniussi, 2013). However, in both of these studies, it is unclear whether the performance improvements are due to perceptual learning or to task learning.

Although the effect of tDCS (frontal stimulation to dorso-lateral prefrontal cortex) on visual working memory has been studied (Zaehle, Sandmann, Throne, Jäncke, & Herrmann, 2011), to our knowledge, no studies have demonstrated any effect of tDCS on consolidation of visual learning as a result of primary visual cortex stimulation. Thus, we sought to examine not only the acute effects of tDCS on visual perception while controlling for day-to-day performance variability, but also to elucidate potential longer-term effects of V1 stimulation on perceptual learning and consolidation.

## 2. Method

### 2.1. Participants

Thirty-one healthy subjects gave written informed consent to participate in this study (mean age: 20.3 years; range: 18–27 years; 10 male; 30 right-handed); six subjects were subsequently excluded from the active stimulation groups because they found the stimulation uncomfortable and one participant was excluded because she failed to bring consistent corrective eyewear over the course of the study. Eight of the remaining 24 subjects received anodal stimulation on Day 1 (A-group), eight received cathodal stimulation on Day 1 (C-group) and eight received sham stimulation on both days (S-group). For the real tDCS groups, tDCS polarity was reversed on Day 2. The three groups did not differ in gender or age. All subjects met the following inclusion criteria: between the ages of 18 and 59 years; no history of neurological or psychiatric conditions; no history of head trauma; no metal implants other than dental fillings; no history of visual disorder or significant refractive error ( $>1$ diopter of cylinder); normal hearing; not currently or possibly pregnant; and no history of other major medical problems. All subjects thus had normal or corrected to normal vision and wore their habitual optical correction, if applicable, throughout the study. Subjects either participated as volunteers or were compensated for their time through class credits assigned through the Sona Experiment Management System (Sona Systems Ltd.). This study was conducted in accordance with the Declaration of Helsinki and was approved by the University of California Los Angeles Institutional Review Board.

### 2.2. Stimuli and apparatus

Participants were seated 50 cm in front of an 18-inch NEC MultiSync 97 F CRT monitor with $1024 \times 768$ px resolution and 100 Hz refresh rate, with their chins resting in a chinrest. The monitor was calibrated for proper gamma correction prior to experiment commencement. The screen background and test stimuli had a mean luminance of 36.2 cd/m$^2$. Stimuli were Gabor patches (sinusoidal gratings within a Gaussian envelope) with a spatial frequency of 16 cycles per degree, a vertical ($0^\circ$) or horizontal ($90^\circ$) orientation and a sigma of $6^\circ$ resulting in a visible area of approximately $13^\circ$. Stimuli were generated and presented using Psykinematix software (KyberVision) which allows for 10.8 bits of contrast resolution by using bitstealing algorithms.

### 2.3. Behavioral procedure

Prior to stimulation days, psychometric functions were measured for all participants using the method of constant stimuli to determine 55%-, 65%-, and 75%-correct contrast detection thresholds. The measurements involved 400 trials (50 trials at each of eight contrast levels: 0,.3,.6,.9, 1.5, 2, 2.5, and 10% contrast) and lasted approximately 40 min including practice. Thresholds were chosen by fitting a Weibull function to each participant's performance across the eight contrast levels and selecting the contrast levels corresponding to 55%, 65%, and 75% correct. These levels correspond to hard, medium, and easy levels of difficulty, and were presented on the two stimulation days during both baseline and stimulation blocks. Day 1 of stimulation took place the day after psychometric functions were measured, and Day 2 of stimulation took place 1–2 days following Day 1. Testing sessions (including baseline and stimulation blocks) lasted approximately 50 min including practice.

On both stimulation days participants first engaged in a practice block to remind them of the task and to allow for adaptation to the dim lighting in the experiment room. During practice, gratings were presented at 0, 40, 50, 60, 70, and 80% contrast. Following practice, participants completed 255 trials of the task (85 trials per easy, medium and hard difficulty level) before and during stimulation. Each block of 255 trials lasted approximately 20 min and difficulty level and grating orientation were randomized within each block. A break was provided mid-way through each block.

During behavioral measurements participants engaged in a two-alternative forced choice (2AFC) task in which they indicated the orientation (vertical or horizontal) of the grating presented in each trial with a key press. Each trial began with a beep accompanied by a central fixation point. The fixation point remained on the screen for 500 ms followed by a Gabor patch stimulus, which was also presented for 500 ms. Following stimulus offset, an asterisk appeared indicating that subjects should respond; the inter-trial interval was fixed at 2 s to ensure consistent timing across measurement sessions. If a participant did not respond within 2 s, the response was recorded as incorrect.

### 2.4. tDCS procedure

tDCS was delivered by a 9 V battery-driven constant DC "$1 \times 1$" stimulator (Soterix Medical, New York, NY) using a pair of carbon electrodes placed inside $5 \times 7$ cm sponges soaked in .9% saline solution, held to the scalp through use of non-conductive plastic straps ("EASYstraps") from the same manufacturer. Thus,

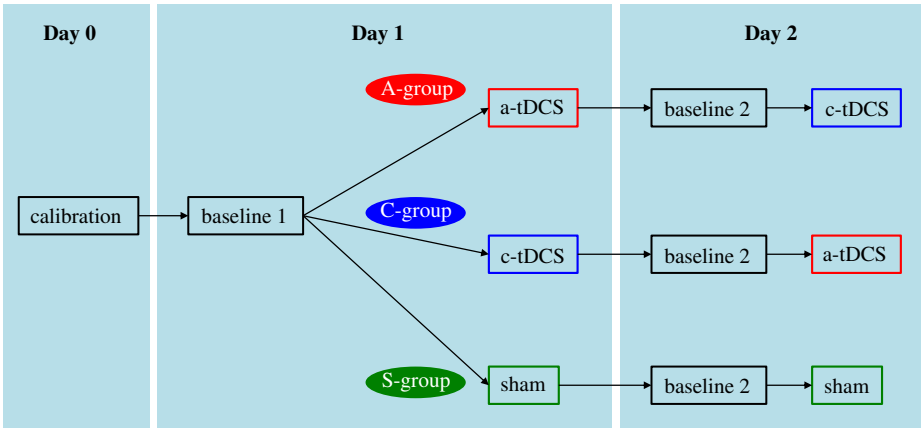


**Fig. 1.** Design of study. All participants underwent calibration and Day 1 baseline, and then were split into A-group, C-group, and S-group.

both active and reference electrodes had an area of 35 $cm^2$ and current density of .57 $\mu A/cm^2$, which is well below the safety limits for tDCS in humans (Nitsche et al., 2003). A single Oz–Cz electrode configuration based on the international 10–20 EEG system was employed, adopted directly from previous tDCS studies related to vision (Antal et al., 2004; Antal et al., 2001, 2003a, b; Antal, Nitsche, & Paulus, 2006; Antal & Paulus, 2008): to stimulate V1, the active electrode was placed 2 cm above the inion along the nasion-inion line (over Oz) and the reference electrode over Cz. Additionally, this montage was recently demonstrated to be especially suited to stimulation of occipital cortex (Neuling, Wagner, Wolters, Zaehle, & Herrmann, 2012).

Because the aftereffects of tDCS for the visual cortex have been shown to be relatively short, and to decay over time (Antal et al., 2003a; Lang et al., 2007), we chose to perform the psychophysical measurements during rather than after stimulation, so as to maximize the stability of any effects of tDCS on within-session performance. Stimulation sessions included 30 s of automatic ramp-up followed by 20 min of stimulation at 2.0 mA, with a similar ramp-down period at the end of the session. During stimulation sessions (Fig. 1), the behavioral procedure did not commence until the stimulation had reached the full 2.0 mA intensity. For the control group who were naive to real stimulation, sham stimulation was accomplished through placing the stimulator in "sham" mode, which mimics the initial ramp-up and final ramp-down but switches the current to .1 mA for the 20 min of stimulation. Thus, all participants believed they were receiving active stimulation due to the tingling sensation on the scalp at the initiation of stimulation.

We avoided conducting the sham control on the same pool of participants that had received active stimulation because a pilot study demonstrated that participants were able to reliably discriminate between real and sham tDCS for a 2 mA current.

Statistical data analyses were performed with the SPSS software (Version 20.0) and Matlab (Version 7.10.0) with the Statistics Toolbox.

## 3. Results

We first performed a 3 (stimulation type: anodal, cathodal, sham) × 3 (difficulty level: hard, medium, easy) mixed design ANOVA, on changes in performance relative to same-day baseline. This analysis revealed no main effect of stimulation type ($F(2,45)=.081$, $p=.92$) or difficulty level ($F(2,90)=.977$, $p=.38$) and no interaction ($F(2,45)=.405$, $p=.85$), indicating no significant differences between baseline and stimulation performance during the same day regardless of stimulation polarity.

Our next analysis focused on performance over time to assess polarity-specific effects on consolidation. Accuracy levels were entered into a 3 (group: A-group, C-group, S-group) × 4 (time: Day 1 baseline, Day 1 stimulation, Day 2 baseline, Day 2 stimulation) × 3 (difficulty: hard, medium, easy) mixed design ANOVA. We found significant main effects for difficulty level ($F(2,42)=137.628$, $p<.001$) and time ($F(3,63)=7.674$, $p<.001$) and a trend for significant effect for group ($F(1,21)=3.377$, $p=.053$), as well as an interaction between group and time ($F(6,63)=3.353$, $p=.006$). No other significant interactions were found (difficulty × group, $F(4,42)=1.126$, $p=.36$; time × difficulty, $F(6,126)=.896$, $p=.50$; time × difficulty × group, $F(12,126)=.894$, $p=.56$), and boxcar analyses revealed no within-session learning.

To explore this interaction between group and time (Fig. 2.1), we performed tests of simple effects. Because no significant effect of stimulation polarity was found in the first ANOVA, we focused on differences in baselines across groups to examine the effect of stimulation on task consolidation (Fig. 2.1). We calculated a baseline difference score for each individual by subtracting baseline performance on Day 1 from baseline performance on Day 2. Further, because we observed no interaction effect with difficulty in any of the previous ANOVAs, we collapsed across the three levels of difficulty. We then performed two-tailed, one-sample *t*-tests to test whether each group's baseline difference scores were significantly different from 0. Results from this analysis revealed that A-group showed no significant differences in baseline performance from Day 1 to Day 2 ($t(7)=.54$, $p>.60$). In contrast, C-group and S-group demonstrated significant improvements from Day 1 to Day 2 on baseline performance, with an average increase in accuracy of 9.68% ($t(7)=5.02$, $p<.005$) and 8.90% ($t(7)=2.409$, $p=.05$), respectively (Fig. 2.2). The difference between the change in performance experienced by A-group and that experienced by the other two groups was large (Cohen's $d=1.6391$ in comparison with the combined C- and S-groups and $d=1.453$ in comparison with S-group only).

To confirm that group differences on Day 2 at baseline were not due to group differences on Day 1 prior to any stimulation, we performed an additional 3 × 3 mixed design ANOVA on Day 1 baseline performance only, with between-subjects factor group (A-group, C-group, and S-group) and within-subjects factor difficulty (hard, medium, easy). This analysis revealed the expected main effect of difficulty ($F(2,42)=47.616$, $p<.001$) but no main effect of group ($F(2,21)=.263$, $p=.77$) and no interaction ($F(4,42)=1.597$, $p=.19$). This indicates that all groups performed equally well at baseline on Day 1. We also performed 3 × 3 mixed design ANOVA to explore whether groups differed in calibrated contrast thresholds, with between-subjects factor group (A-group, C-group, and S-group) and within-subjects factor contrast threshold (55%-, 65%-, and 75%-correct contrast threshold). This analysis revealed only the expected main effect of threshold level ($F(2,42)=142.420$, $p<.001$) but no effect of group ($F(2,21)=.786$, $p=.469$) and no interaction ($F(4,42)=2.048$, $p=.11$), thus confirming that learning differences are not due to any group differences in detection thresholds.

Next, we explored the potential reasons for the difference between the findings of some previous studies (anodal stimulation benefitting performance and cathodal stimulation hurting performance) and our findings. Specifically, previous studies that had reported a benefit in performance during anodal stimulation had

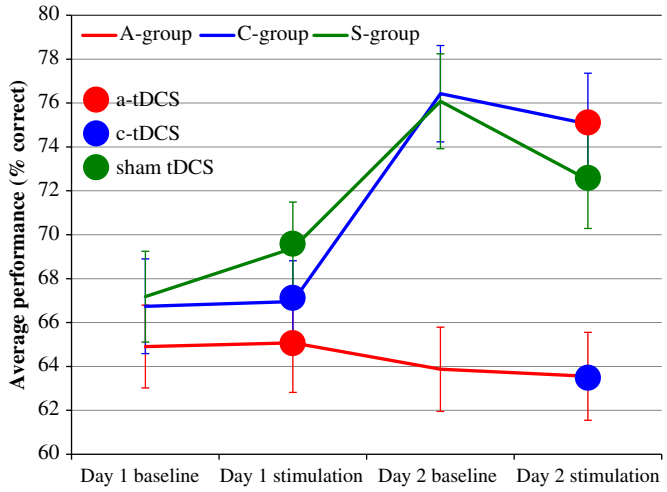


**Fig. 2.1.** Performance of each participant group as a function of time, collapsed across difficulty level.

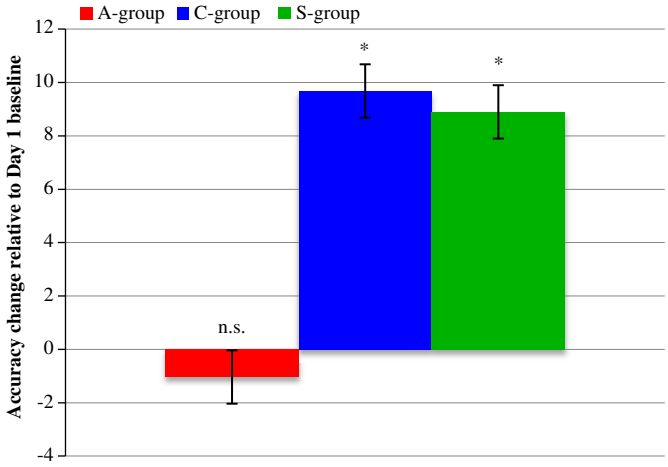


**Fig. 2.2.** Differences in baseline performance from Day 1 to Day 2 by group, collapsed across difficulty level. Stars indicate significance of one-tailed *t*-test ($p < .05$).

compared the performance with the baseline performance collected on a previous day. We sought to test whether the comparison with a prior-day baseline vs. comparison with the same-day baseline could explain the differential findings. We thus computed all difference scores relative to the Day 1 baseline (Fig. 2.3) collapsed across difficulty level: for each subject, Day 1 baseline performance was subtracted from stimulation performance under a-tDCS, c-tDCS, and s-tDCS collapsed across stimulation order and day. This analysis parallels the approach of comparing performance under stimulation conditions to a separate baseline taken during a prior session, as conducted by Antal et al. (2001). We then conducted two-tailed, one-sample *t*-tests on the difference scores (comparing them to 0, i.e., no change). Accuracy during cathodal stimulation was not significantly lower than Day 1 baseline ($t(15)=.36$, $p=.723$). However, accuracy during anodal stimulation was on average 4.24% better than Day 1 baseline, a significant improvement ($t(15)=2.43$, $p=.028$) amounting to a medium effect size (Cohen's $d=.63$). Interestingly, there was also a trend for improved accuracy during sham stimulation ($t(15)=2.04$, $p=.059$). These findings qualitatively replicate the general "anodal-enhancement, cathodal-decrement" pattern of results demonstrated by many other groups

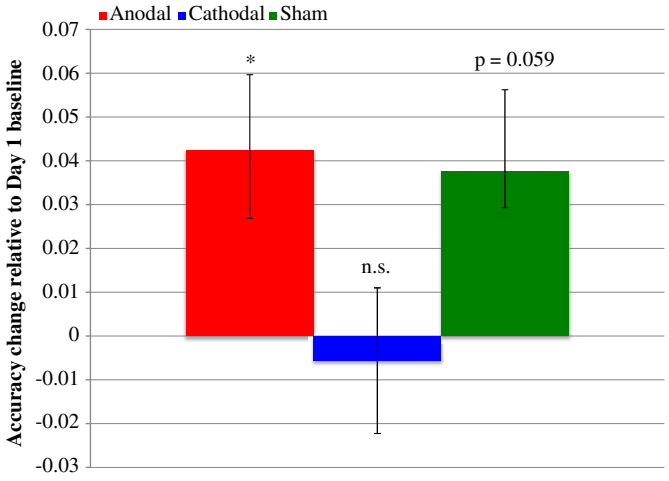


**Fig. 2.3.** Difference scores (stimulation–baseline) for performance under a-tDCS, c-tDCS, and sham stimulation relative to first day baseline. Stars indicate significance of one-tailed *t*-test ($p < .05$).

(e.g., Antal et al., 2001; Olma, Kraft, Roehmel, Irlbacher, & Brandt, 2011).

## 4. Discussion

Our results demonstrate that participants who received anodal stimulation on Day 1 experienced no improvements in performance on Day 2, while those who received cathodal and sham stimulation on Day 1 showed a significant increase in performance on Day 2. This suggests that anodal tDCS blocked task learning.

Further, unlike several previous studies of contrast thresholds (e.g., Antal et al., 2001; Kraft et al., 2010), we did not observe a change in performance during stimulation (improvement by anodal or impairment by cathodal) relative to same-day baseline. However, when performance during stimulation was compared to Day 1 baseline only, this typical pattern did emerge: a-tDCS did appear to provide significant benefit to performance. This discrepancy between conclusions for the single- versus double-baseline analyses highlights the importance of taking a separate baseline measurement of task performance on each day of a multi-day intervention study so as to control for day-to-day changes in performance due to factors outside experimental conditions, as well as the potential effect of repeated stimulation of the same or opposite polarity within a 24-hour window (see e.g. Monte-Silva, Kuo, Liebetanz, Paulus, & Nitsche, 2010). To our knowledge, only one other study of the effects of tDCS on contrast sensitivity collected daily baseline measurements (Kraft et al., 2010); although they, too, report the typical anodal enhancement, they also report no interaction between learning and stimulation polarity. However, their stimulation sessions occurred at least seven days apart, so the offline effects we observed here might have dissipated or been masked by normal forgetting. Other differences between threshold perimetry and our contrast detection task, as well as specifics of their stimulation schedule, could also account for discrepancies between their results and ours.

The alteration of offline effects via external modulation of cortex observed in the current study is consistent with results demonstrated in the motor task learning domain. Impaired consolidation (measured by increased errors) as a result of a-tDCS has been demonstrated in an explicit motor learning task (Lang, Nitsche, Sommer, Tergau, & Paulus, 2003). The current study is the first to demonstrate any such offline effects of external modulation in the visual cortex. However, a number of studies

have reported that a-tDCS to V1 can cause online perceptual improvements in both task performance and learning (see e.g. Antal et al., 2003a, b). How then could a-tDCS lead to impairment in overnight consolidation? One plausible explanation for our results is the presence of homeostatic plasticity mechanisms in V1. It has been demonstrated that a-tDCS to M1 can result in the engagement of homeostatic mechanisms that maintain cortical excitability within an optimal range and prevent excess levels of neural activity (Siebner et al., 2004). In that study, 1 mA a-tDCS was applied to M1 for 10 min, followed by application of rTMS. It was found that a-tDCS led to subsequent reduction in corticospinal excitability via rTMS, while c-tDCS resulted in the opposite effect. This result suggests that by initially increasing the resting membrane potential, a-tDCS resulted in engagement of inhibitory homeostatic mechanisms to reduce over-excitability (that would otherwise be induced by rTMS) in the affected area. A follow-up study demonstrated a qualitatively similar (albeit smaller) effect in V1: a short-lasting increase in phosphene threshold was revealed when a-tDCS was followed by rTMS, evidence that a-tDCS had engaged inhibitory homeostatic plasticity mechanisms (Lang et al., 2007). No such priming effect was demonstrated for cathodal or sham tDCS. This pattern could explain our finding of impaired consolidation due to a-tDCS and suggests that a-tDCS may have engaged inhibitory homeostatic mechanisms, resulting in reduced plasticity and consequent prevention of effective LTP. This blocking of LTP, in turn, would not necessarily result in performance decrements during the task itself, but rather in prevention of learning trace development and subsequent overnight consolidation. Indeed, the engagement of homeostatic plasticity mechanisms have been used to explain why tRNS produced facilitation of orientation discrimination perceptual learning but a-tDCS did not (Fertonani et al., 2011).

Another possibility is that a-tDCS adds “noise” to the signal within V1. Anodal tDCS has been shown to raise resting membrane potentials, leading to higher spontaneous firing rates (Siebner et al., 2004), in addition to higher spike rates in response to stimuli. This argument has been called upon to explain the lack of consolidation in an explicit motor learning task (Lang et al., 2003), contrasting to the enhancement of consolidation observed in a motor skill learning task (Reis et al., 2009). As in the current study, Lang and colleagues observed no polarity-specific effect during task learning, and only observed significant polarity-dependent effects when consolidation was examined at least one week after stimulation had been completed (Lang et al., 2003). They postulated that increased baseline levels of neural activity leading to a decreased signal to noise ratio could explain this effect. A poorer signal-to-noise ratio might prevent development of an appropriate learning trace that could later be consolidated, leading to the absence of overnight learning that we observed. The argument that increased background neural activity can reduce the signal to noise ratio is supported by studies indicating that background activity is not entirely random and may contain meaningful structure (Faisal, Selen & Wolpert, 2008; Lochmann & Deneve, 2011). In contrast, c-tDCS, like sham, may preserve the existing signal-to-noise ratio. Note that explanations based on the engagement of inhibitory homeostatic plasticity mechanisms and degradation of the signal-to-noise ratio are not mutually exclusive.

Despite the plausibility of these mechanisms, several other potential explanations of the blocking effect of a-tDCS to V1 found in this study should not be ignored. For example, it has been shown that a-tDCS to dorsolateral prefrontal cortex (DLPFC) and M1 can improve performance on a cognitive set-shifting task, while c-tDCS to the same areas impeded performance on a motor set-shifting task (Leite, Carvalho, Fregni, & Gonçalves, 2011). Because successful performance on our task involves not only detection but also resolution of the visual stimuli, it is possible that a-tDCS resulted in facilitated set-shifting and, consequently, decreased focus on the current task. Furthermore, cathodal stimulation to MT+ has been argued to improve performance on a complex visuomotor tracking task through increasing focus (Antal et al., 2004). Thus it is conceivable that lack of focus due to anodal stimulation may have played a role in our results.

Of course, it is possible that tDCS may have affected functional connectivity to other task-relevant cortical regions. For example, there is evidence to suggest that increased activity in networks of brain areas outside M1 is associated with explicit finger sequence learning (Honda et al., 1998); it is therefore possible that active stimulation to V1 ultimately served to alter the functional connectivity between V1 and other task-relevant areas, leading to the observed lack of learning. It is also possible that the reference electrode, positioned at Cz, resulted in unintended excitability changes in somatosensory or motor cortex, although it is unclear how such changes might have affected perceptual learning or consolidation. Finally, it cannot be ruled out that the current flowing between the two electrodes did not, in fact, lead to effects in some non-target cortical structure.

## 5. Conclusions

In this study, we report the novel finding that anodal tDCS to V1 can block normal perceptual learning, specifically offline effects and consolidation, of a visual contrast detection task. We speculate that the observed effect is due to anodal tDCS either activating inhibitory homeostatic plasticity mechanisms in V1 and nearby structures, or increasing baseline activity degrading the signal-to-noise ratio, which would mask any learning trace. These findings are the first to demonstrate that tDCS can modulate overnight consolidation of visual perceptual learning.

## Acknowledgments

We thank Felipe Fregni for helpful discussions. MP was supported by an NSF graduate research fellowship. BT was supported by the Marsden Fund of New Zealand. LS was supported by NSF Grant 1057969.

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