Brain Stimulation 10 (2017) 773–779

Contents lists available at ScienceDirect

Brain Stimulation

journal homepage: http://www.journals.elsevier.com/brain-stimulation

Anodal and cathodal electrical stimulation over V5 improves motion perception by signal enhancement and noise reduction

Luca Battaglini [a], [*], Stefano Noventa [b], Clara Casco [a]

[a] Department of General Psychology, University of Padova, Via Venezia 8, 35131, Padova, Italy
[b] Hector Research Institute of Education Sciences and Psychology, Eberhard Karls Universität Tübingen, Tübingen, Germany

A R T I C L E I N F O

Article history:
Received 26 February 2017
Received in revised form
17 April 2017
Accepted 24 April 2017
Available online 28 April 2017

Keywords:
tDCS
Random dots
Coherent motion
Signal enhancement
Noise reduction

A B S T R A C T

Background: The effect that transcranial direct current stimulation (tDCS) has on discrimination of coherent motion (CM) signals in a field of randomly moving dots (noise) can be accounted for by both noise reduction and signal enhancement.
Objective: To distinguish between noise reduction and signal enhancement, we monitored the discrimination of the correct CM direction as a function of the coherence level (using the psychophysical method of constant stimuli). We then analyzed the threshold and slope parameters.
Method: Thirty observers participated in the experiment; fifteen received cathodal stimulation, and fifteen received anodal stimulation, all over left V5.
Results: The results showed that, rather than having opposite effects on CM discriminability, the positive- and negative-polarity tDCS over V5 affected the two parameters differently. When compared to a sham stimulation, anodal tDCS reduced the threshold, thus indicating signal enhancement. On the other hand, cathodal tDCS reduced the steepness of the slope (with better performance at low levels of coherence) compared to the sham stimulation, thus indicating noise reduction. Moreover, the results showed that late perceptual learning improved the participants' performance at medium/high CM similar to what anodal tDCS did.
Conclusion: These results suggest a dissociation between the neural mechanisms responsible for enhanced CM discriminability: reduction of noisy or uncorrelated motion by cathodal tDCS versus increased activation of weakly correlated motion signals by anodal tDCS or perceptual learning.

Introduction

Transcranial current stimulation (tES) has been extensively investigated in the past decade, as it offers a noninvasive and safe method to change cortical excitability. It alters neurons' spontaneous firing rates, leading to changes in synaptic efficacy and modulations of the responses to afferent signals [1–4]. One such type of stimulation, transcranial direct current stimulation (tDCS), generally induces opposite changes in spontaneous activity: Cathodal stimulation (c-tDCS) decreases cortical excitability, whereas anodal stimulation (a-tDCS) increases it. However, the modulation of neural activity by tDCS is far more complex than such a simplistic view would imply [5,6]. In particular, the role of tDCS in the detection and discrimination of visual stimuli is currently under debate. The inhibitory effect that c-tDCS has on visual perception is inferred from the findings that c-tDCS increases psychophysical thresholds in visual tasks [7–10] and reduces visual noise [11].

However, these psychophysical data are not always consistent with the modulatory effects that c-tDCS has on the amplitude of the visual evoked potential (VEPs) components that these tasks elicited [10,12,13]. The a-tDCS effect appears to be even less obvious. For example, the psychophysical data showed that a-tDCS reduced the suppressive effects of a visual surround [14]; however, it had a null effect in a contrast sensitivity task [7] and in a visuomotor task [11]. In addition, a-tDCS has been reported as having both facilitatory [10,13] and inhibitory [12] neural correlates to the visual response. These apparently contradictory findings suggest that the effect of tDCS depends on the interaction of the activity in the stimulated area and the task characteristics [15].

Coherent motion (CM) is a stimulus that is often used to investigate the effect of tDCS on perception [11]. Perception of CM is typically obtained by presenting a field of small, moving dots, some

---

* Corresponding author.
E-mail address: luca.battaglini@unipd.it (L. Battaglini).

http://dx.doi.org/10.1016/j.brs.2017.04.128

of which coherently move in the same direction as the rest move randomly. Dots carrying a specific motion signal are correlated in both space and time, as they are replotted with a fixed spatial offset after a fixed temporal interval; they thus generate a global motion percept [16]. Antal and colleagues [11] found that tDCS did not have a complementary effect on MT+/V5 in the condition of coherently moving dots; although c-tDCS enhanced performance, a-tDCS had no effect. They suggested that, in the presence of uncorrelated motion, the effect of a-tDCS cannot be detected; this is likely because the increase in cortical excitability enhances the response to both correlated and uncorrelated signals, leaving the signal-to-noise ratio unchanged. However, c-tDCS improved performance, as expected; it decreased the global excitation level, depressing the uncorrelated motion so that it was under the threshold while leaving the correlated motion above the threshold [11].

Because both the psychometric response in the sensory system and the neurometric response in the MT+/V5 neurons are often described by sigmoid functions [17–19], one might question whether the effects of c-tDCS and a-tDCS would occur at different coherence levels, ranging from chance to ceiling performance. Antal and colleagues [11] looked at the effect that tDCS had in a CM task on one point of the function. They found that a-tDCS had an effect under 100% coherence, a condition that reflects the response to a single neuron's preferred direction rather than the weighted response of both preferred and null directions [18].

Investigating the accuracy of the data relative to a wide range of coherence levels reveals information about how c-tDCS and a-tDCS affect performance at both low and high coherence levels. The simplest prediction is that a single mechanism accounts for the effects of both c-tDCS and a-tDCS, thus affecting discriminability in opposite ways by (respectively) increasing and decreasing the threshold parameter. However, an intriguing hypothesis is that the effects of c-tDCS and a-tDCS result from different mechanisms, with c-tDCS enhancing discriminability by selectively modulating the response to uncorrelated motion (with low signal-to-noise ratios) and a-tDCS doing so by selectively modulating CM (with medium to high signal-to-noise ratios).

At low coherence levels, one prediction is that c-tDCS will reflect into a less steep psychometric function [11] (because of its better performance at lower levels of CM) and will have little or no effect on the threshold [20] when the data are fitted. The slope change reflects the system's dynamic range of coherence; a steeper slope indicates a more restricted dynamic range [20]. On the other hand, a-tDCS modulation of the response to correlated motion signals is predicted to reflect into a lower threshold but have almost no effect on the slope. To test these predictions, we analyzed the individual performance with a combination of parametric methods [21], nonparametric methods [22], and signal-detection theory [23].

Method

Participants

Thirty healthy students with normal or corrected-to-normal vision were recruited from the University of Padova. Exclusion criteria included history of psychiatric disorders, drug abuse, active medication, pregnancy, and susceptibility to seizures. Participation in the study was voluntary, and individuals were naïve to both the experimental procedure and the purpose. Participants were randomly assigned to one of two groups: c-tDCS (seven males and eight females) and a-tDCS (eight males and seven females). Informed consent was obtained from all participants, and the study was conducted in accordance with the Declaration of Helsinki (1964). The experimental methods received ethical approval from the University of Padova (protocol 1756).

Stimuli and apparatus

Participants were placed in a dimly dark room and seated 57 cm away from the display screen. Viewing was binocular. Stimuli were generated with Matlab Psychtoolbox [24–26] and displayed on a 19-inch Asus monitor with a refresh rate of 60 Hz. The screen resolution was set to 1920 × 1080 pixels, and each pixel subtended ~1.5 arcmin. The luminance of the background was 0.7 cd/m^2. The stimulus was a square window of 10 deg that was filled with 200 moving white dots, each 0.075 deg in diameter (density: 2 dots/deg^2). CM resulted from a temporal sequencing of 8 frames: In the first frame, the dots were randomly positioned within the square window, and they were then displaced by 0.05 deg in each subsequent frame (i.e., Brownian motion [27]), producing a speed of 3 deg/s. The stimulus was displayed 10 deg to the left or to the right of the center of the screen for 133 ms (8 frames at a frame duration of 16.67 ms). The stimulus duration was short enough to prevent both covert attentional tracking and saccadic eye movements toward the target position [28–30]. The dots had a limited lifetime; in each frame, 1/5 of them were reallocated to a random position, so the maximum dot lifetime was 83.3 ms. In addition, moving dots that traveled outside the window were replaced by new dots at different, randomly selected locations within the square window, thus keeping the density constant.

The dots' coherence (motion in the same direction) varied at seven levels across the trials: 10, 20, 30, 40, 50, 60 and 70%. The direction of the coherently moving dots was randomly fixed as being upward or downward; the other dots moved in random directions.

Procedure

After a few practice trials to become familiar with the task, the participants performed two experimental sessions on the first day (Day 1). Each session consisted of a 12-min stimulation interval, immediately followed by the CM discrimination task. The two sessions were devoted to either c-tDCS or a-tDCS (depending on the group) and to sham stimulation. The order of the stimulation sessions was randomized. The same procedure was repeated during the same hour on Day 2 so to check the effect of tDCS within a 24-h interval. The left hemifield was stimulated and the psychophysical task was performed with stimuli that were randomly presented in either the left or the right hemifield. The method of constant stimuli was used to fit the psychometric function, modeling the relationship between the motion-direction discrimination and the coherence levels. Each of the four blocks consisted of 140 trials: 7 levels of coherent dots × 2 positions (right and left) × 10 repetitions; the total duration (stimulation + task) was about 23 min. In each trial, the participants were required to fixate on a white cross that was placed at the center of the screen. The stimulus then randomly appeared for 133 ms to the left or to the right of the fixation point; this stimulus duration was too short to allow for saccadic eye movement toward the target position. The participants' task was to indicate (by pressing a button) whether the coherent dots moved upward or downward.

Transcranial direct current stimulation

A battery-driven constant-current stimulator (BrainStim, EMS) delivered the tDCS through a pair of conductive rubber electrodes in a 5- to 7-cm water-soaked synthetic sponge. The electrode montage comprised one over the vertex (Cz), as in previous studies [11,12,31], and another over left V5/MT (3 cm above and 5 cm to the left of the inion); the polarity refers to V5/MT (V5/MT − Cz montage). The tDCS and sham stimulations were applied, in a randomized order, for 12 min each (+30 s of fade in/out) at an intensity of 1.5 mA. In the sham session, the current was delivered only for the first 30 s and the last 30 s of the 12-min session. After 24 h, the participants were retested with the same protocol.

Statistical analysis

As a first step, the individuals' data were fitted to the proportions of correct CM discrimination as a function of coherence levels. However, the logistic function-fitting [21] did not converge to suitable estimates for the parameters; it generated negative estimates for a few individuals. Therefore, threshold parameters (α) were estimated individually by means of the Spearman-Kärber method, which is a reliable nonparametric method for estimating threshold values without assumptions about the nature of the psychometric functions (for an application to the two-alternative forced choice (2AFC) case, see Ref. [22]). The slope-parameter estimation was instead performed within a signal detection framework through an analysis of the linear fitting [32] of the discriminative sensitivity (*d'*) in the 2AFC case. Correct responses with upward CM were considered hits, and reports of upward CM when the coherent dots were moving downward were considered false alarms (see, e.g., Macmillan and Creelman [23]).

Results

Effect of c-tDCS

The results shown in Fig. 1 indicate that the threshold is unaffected by c-tDCS and that the slope is less steep in the right visual field when left MT+/V5 was stimulated than when was not stimulated (sham). This suggests c-tDCS provides selective improvement in motion-direction discrimination at low signal-to-noise ratios. Such a result is well-expressed by the slopes of the *d'* data as a function of coherence levels. Table 1 shows the averages and SDs of the threshold (α) parameters, as estimated using the Spearman-Kärber method, and the averages and SDs of the slope parameters obtained for *d'* divided by day, laterality, and tDCS conditions (sham vs. c-tDCS).

ANOVA was conducted on the estimated thresholds that were obtained using the Spearman-Kärber method, with the Day (Day 1 vs Day 2), Laterality (right vs. left), and tDCS (sham vs. c-tDCS) as the main factors. Only the factor Day had an effect ($F_{(1,14)} = 11.37$; $p = 0.005$; $\eta^2_p = 0.45$).

The ANOVA carried out on the slopes fitted to *d'* revealed a significant effect of tDCS ($F_{(1,14)} = 8.1$; $p = 0.013$; $\eta^2_p = 0.37$) and a significant interaction of tDCS × Laterality ($F_{(1,14)} = 7.77$; $p = 0.015$; $\eta^2_p = 0.36$). Bonferroni-corrected pairwise comparisons indicated that the slopes, when linearly fit to *d'*, were less steep in the tDCS

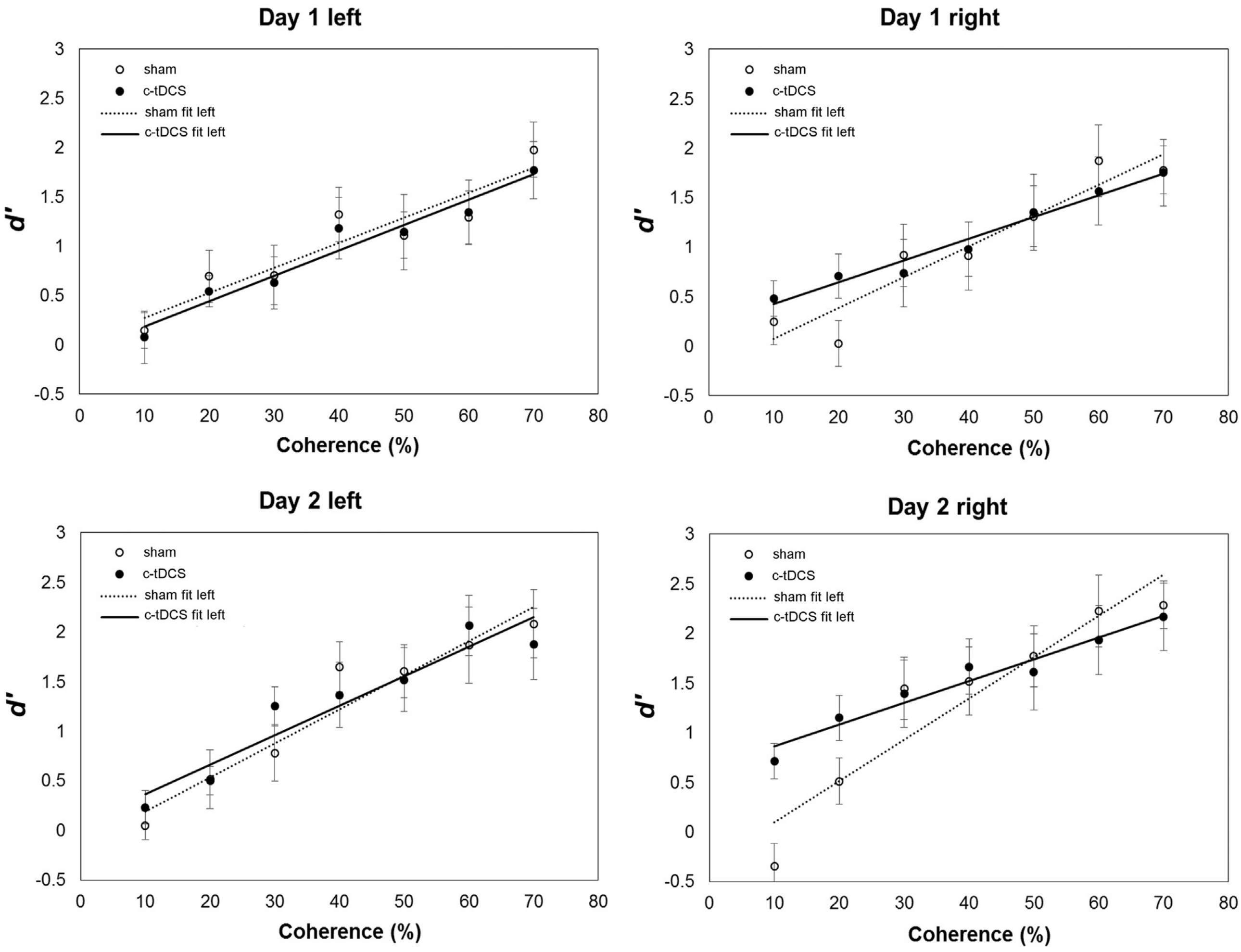

Fig. 1. ***d'***. Each graph compares the linear fittings of the *d's* obtained in the sham and c-tDCS conditions. Empty circles represent the mean *d'* values for the 15 participants in the sham condition, and black circles represent the mean *d'* values obtained with c-tDCS. Left and right indicate the positions of the stimuli in the visual field.

Table 1
The average values of the *α* (threshold) and *β* (slope) parameters and their estimated standard deviations are calculated with the Spearman-Kärber method and with the linear fitting of *d'*. The values are divided into day, laterality, and c-tDCS conditions.

	Day 1				Day 2			
	α SK	SD *α SK*	*β d'*	SD *β d'*	*α SK*	SD *α SK*	*β d'*	SD *β d'*
s-left	54.3	5.1	0.25	0.17	45.1	4.7	0.34	0.18
t-left	55	5.2	0.26	0.24	47	4.5	0.29	0.19
s-right	54.3	5.2	0.31	0.27	45.9	4.8	0.42	0.16
t-right	51.26	5.2	0.22	0.17	40.6	4.7	0.22	0.22

than in the sham condition, but only when the stimulus was presented in the right visual field ($p < 0.001$). Analyses of the criterion C did not reveal any significant effect.

Finally, the effect that stimulation order had on thresholds and slopes was analyzed with an ANOVA that had one between-subjects factor (the Order: tDCS-sham vs. sham-tDCS) and two within-subjects factors (Laterality and tDCS). Neither the main Order effect nor its interactions were significant.

These results indicate a selective effect of c-tDCS at low signal-to-noise ratios, which in turn suggests that noise reduction increases motion-direction discriminability.

Effect of a-tDCS

Fig. 2 shows higher *d'* for a a-tDCS than in the sham stimulation when the stimulus is presented in the right visual field, especially at medium and high levels of coherence. This result is compatible with a threshold reduction (but no change in slope) in the stimulation condition. Table 2 shows the averages and SDs of the slopes and thresholds for each day, laterality, and tDCS condition.

As for the c-tDCS data, repeated-measures ANOVAs were performed with the Day, Laterality, and tDCS as main factors. The ANOVA of the threshold data shows significant effects for Day ($F_{(1,14)} = 8.77$; $p = 0.01$; $\eta^2_p = 0.39$), laterality ($F_{(1,14)} = 5.8$, $p = 0.004$, $\eta^2_p = 0.29$), and tDCS ($F_{(1,14)} = 12.12$; $p = 0.004$; $\eta^2_p = 0.46$). More importantly, the tDCS × Laterality interaction is significant ($F_{(1,14)} = 11.9$; $p = 0.004$; $\eta^2_p = 0.46$), indicating lower thresholds for tDCS than in the sham, but only when the stimulus was presented in the right visual field ($p < 0.001$).

The ANOVA for the slopes of the data linearly fit to *d'* (Fig. 2) revealed an effect only for Day ($F_{(1,14)} = 22.76$; $p < 0.001$; $\eta^2_p = 0.61$), thus indicating steeper slopes on Day 2 than on Day 1. Analyses of the criterion C did not reveal that the stimulation had any significant effect. Finally, the effect that the stimulation order had on the thresholds and slopes was analyzed with an ANOVA that

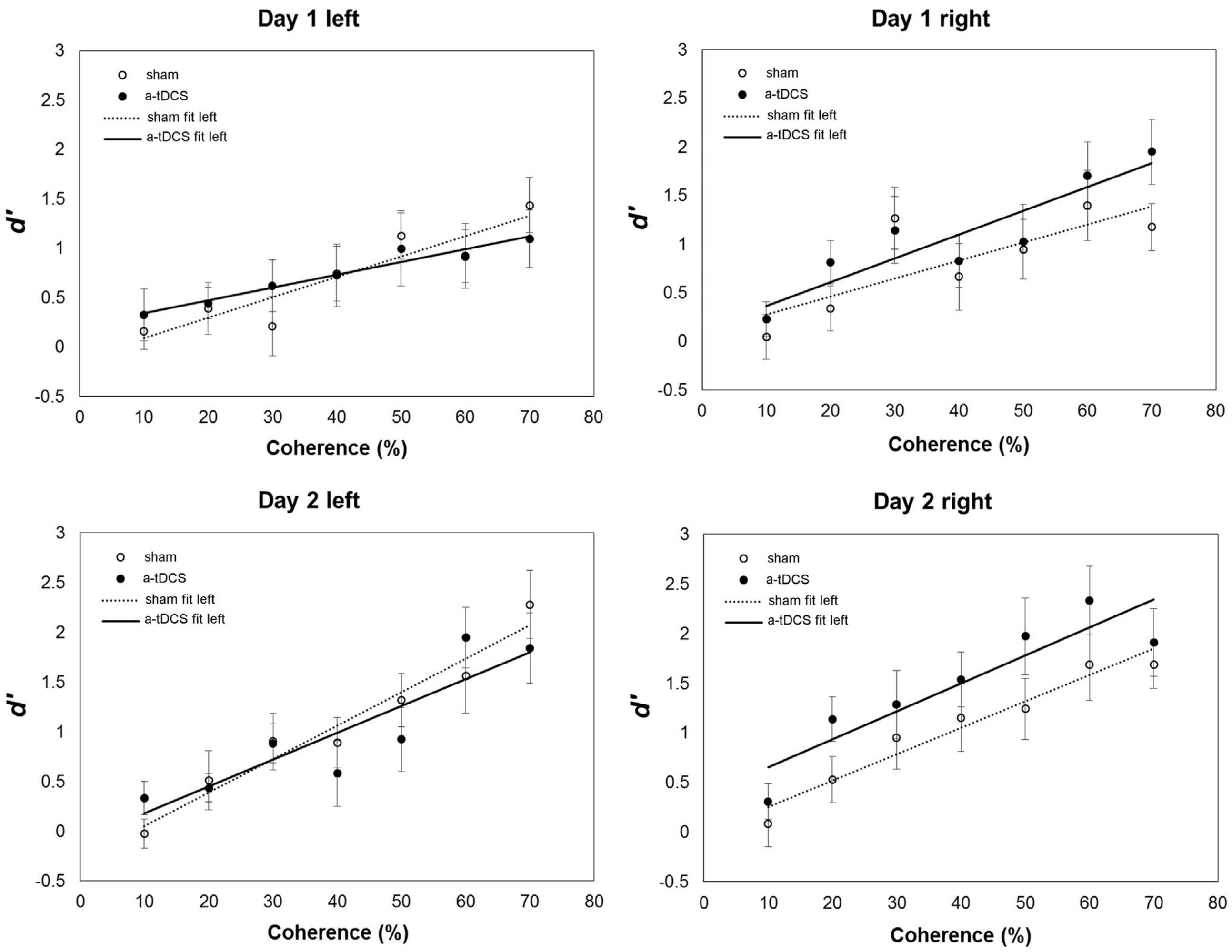

Fig. 2. ***d'***. Each graph compares the linear fittings of the *d's* obtained in the sham and a-tDCS conditions. Empty circles represent the mean *d'* values for the 15 participants in the sham condition, and black circles represent the mean *d'* values obtained with a-tDCS. Left and right indicate the positions of the stimuli in the visual field.

Table 2
The average values of the α (threshold) and β (slope) parameters and their estimated standard deviations are calculated with the Spearman-Kärber method and with the linear fitting of *d'*. The values are divided into day, laterality, and a-tDCS conditions.

	Day 1				Day 2			
	α *SK*	SD α *SK*	β *d'*	SD β *d'*	α *SK*	SD α *SK*	β *d'*	SD β *d'*
s-left	62.8	5.64	0.21	0.16	57.1	5.01	0.33	0.17
t-left	60.8	5.79	0.13	0.23	55.8	5.39	0.27	0.18
s-right	62.3	5.77	0.19	0.18	58.2	5.29	0.27	0.16
t-right	50.46	4.71	0.25	0.19	44.2	5.01	0.28	0.19

used one between-subjects factor (the Order: tDCS-sham vs. sham-tDCS) and two within-subjects factors (Laterality and tDCS). Neither the main order effect nor its interactions were significant.

Thus, as with c-tDCS, a-tDCS increases CM discriminability; however, unlike c-tDCS, a-tDCS has an overall effect.

Polarity effects

The distinct effects of c-tDCS and a-tDCS were further analyzed using a mixed-design ANOVA with Group (a-tDCS vs. c-tDCS) as a between-subjects factor and with Stimulation (sham vs. real), Laterality (left vs. right), and Day (Day 1 vs. Day 2) as within-subjects factors. The ANOVA for the threshold values obtained with the Spearman-Kärber method revealed significant effects for Day ($F_{(1,28)} = 19.65$; $p < 0.001$, $\eta^2_p = 0.4$), Laterality ($F_{(1,28)} = 8.17$; $p = 0.008$; $\eta^2_p = 0.23$), and Stimulation ($F_{(1,28)} = 7.07$; $p = 0.013$; $\eta^2_p = 0.2$). The Group × Laterality × tDCS interaction did not reach overall significance ($F_{(1,28)} = 1.97$; $p = 0.17$; $\eta^2_p = 0.07$); however, the planned (Bonferroni-corrected) *t*-test comparisons showed that the group stimulated with a-tDCS in the right visual field obtained lower thresholds than it did in the sham stimulation ($p < 0.001$).

The ANOVA for the slopes showed significant effects for Day ($F_{(1,28)} = 13.99$; $p = 0.001$; $\eta^2_p = 0.33$) and Stimulation ($F_{(1,28)} = 6.2$; $p = 0.019$; $\eta^2_p = 0.18$). Moreover, there was a significant three-way Group × Laterality × tDCS interaction ($F_{(1,28)} = 8.48$; $p = 0.007$; $\eta^2_p = 0.23$). Pairwise (Bonferroni-corrected) *t*-test comparisons show that, only for the group that was stimulated with the c-tDCS, the slope was shallower with real stimulation in the right visual field than with sham stimulation ($p = 0.04$). This suggests that, when the stimulus was presented in the right visual field, c-tDCS reduced slope steepness but a-tDCS did not.

Perceptual learning effects

The effects of tDCS may interact with perceptual learning (PL). A possibility is that tDCS effects are boosted by perceptual learning (PL). We addressed this issue in two ways.

First, we disentangled the effects of PL and tDCS. Because we obtained no tDCS effect when the stimulus was presented in the left visual field, we used the thresholds and slopes obtained in this condition to further investigate the early (within-day) and late (cross-day) PL effects. To this end, we computed both early-$PL_{modulation}$ and late-$PL_{modulation}$ for the thresholds and slopes: early-$PL_{modulation} = \log_{10}(Block2/Block1)$ and late-$PL_{modulation} = \log_{10}(Day2/Day1)$. For the threhsolds a value of $PL_{modulation} < 0$, when confirmed by a one-sample *t*-test, indicates that the PL improves performance; whereas a $PL_{modulation} > 0$ indicates impaired performance. The results showed that the early-$PL_{modulation}$ never differed from 0, indicating the absence of early-$PL_{modulation}$ on both days (Day1 and Day 2) and in both groups (a-tDCS and c-tDCS). However, when the data were averaged across blocks and used to compute late-$PL_{modulation}$, an effect was found (Fig. 3); the late-$PL_{modulation}$ of the threshold was significantly lower than 0 ($t_{(29)} = 2.64$; $p = 0.013$). The late-PL modulation was further confirmed by the result of a steeper *d'* slope (indicating better performance) on Day 2 ($t_{(29)} = 3.41$; $p = 0.002$).

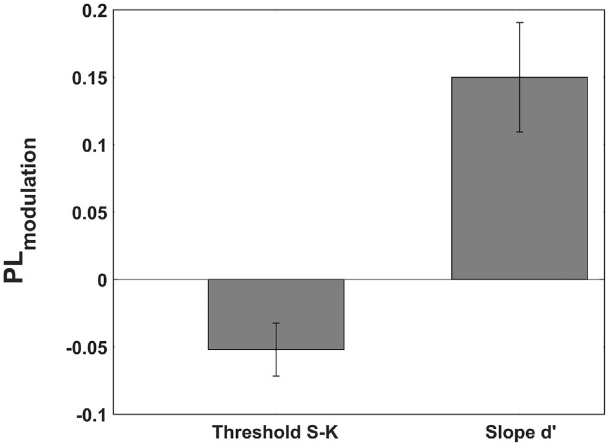

Fig. 3. PL modulation. The PL modulation—$\log_{10}$(Day2/Day1)—is calculated for the thresholds (using the Spearman-Kärber method) and for the slopes of the *d'* linear fitting. The PL modulation for the thresholds is negative, indicating a threshold reduction from Day 1 to Day 2.

Second, we assessed whether the tDCS interacted with the early-$PL_{modulation}$. To this end, the early-$PL_{modulation}$ of both thresholds and slopes, which were obtained for the various day, group, laterality, and stimulation-order conditions, were analyzed using one-sample *t*-tests. In the c-tDCS group, the early-$PL_{modulation}$ of the thresholds never differed from 0, and the early-$PL_{modulation}$ of the slopes was significant only on Day 2 and only with the stimulus presented in the right visual field. Indeed, in this condition, we obtained a $\log_{10}$(sham/tDCS) higher than 0 ($t_{(8)} = 2.7$; $p = 0.027$) in Block 1, indicating relatively flat slopes with tDCS; we also obtained a $\log_{10}$(tDCS/sham) lower than 0 ($t_{(5)} = 3.7$; $p = 0.013$) in Block 2, indicating, again, relatively flat slopes with tDCS.

With anodal stimulation, we found an early-$PL_{modulation}$ of thresholds but not of slopes. Indeed, for thresholds, the $\log_{10}$(sham/tDCS) was higher than 0 in Block 1, an effect that reached significance on Day 1 ($t_{(8)} = 2.85$; $p = 0.021$). On the other hand, the $\log_{10}$(tDCS/sham) was lower than 0 in Block 2, an effect that reached significance on Day 2 ($t_{(5)} = 2.97$; $p = 0.031$). Both these effects indicated a relatively low threshold with tDCS. Altogether, these results indicated that the tDCS affected the performance regardless of the stimulation order, thus confirming that no within-day PL occurred.

Discussion

To assess the effects of tDCS over left MT+/V5, participants took part in a 2AFC task in which they had to discriminate CM direction (up vs. down). Slopes and thresholds were estimated in relation to stimulation type (sham vs. tDCS), visual field presentation (left vs. right) and day (Day 1 vs. Day 2). The results revealed that, for stimuli presented to the right of the fixation point on Day 2, c-tDCS produced a modulation of the slope of the linear fitting [32] for discriminative sensitivity, but not for the threshold. This indicated that the stimuli improved accuracy at low levels of coherence, with high noise with respect to the signal. Conversely, for the same stimulus position, a-tDCS led to threshold reduction, as estimated by the Spearman-Kärber method. The different effects of c-tDCS and a-tDCS stimulation on threshold and slope were further highlighted in a direct investigation of the polarity effect and through a comparison of the sample performances in the two stimulation conditions. The analysis carried out with regard to *d'* and the effects produced by the stimulation's polarity had the same results.

By analyzing performance as a function of coherence levels [17,18,33,34], we demonstrated, for the first time, that both a-tDCS and c-tDCS improve CM discriminability. In addition, we found a dissociation in the modulatory effects of a-tDCS and c-tDCS in CM discrimination. These results ruled out the most obvious hypothesis in which, if c-tDCS reduces noise, a-tDCS increases it (thus reducing CM discriminability). Alternatively, our results suggested that the improved discriminability of a-tDCS and c-tDCS were due to different mechanisms. In agreement with previous researchers [11], we suggest that the c-tDCS-dependent improvement might be explained by c-tDCS reducing the firing rate, thus depressing the uncorrelated motion under the threshold and leaving the correlated motion above the threshold (and consequently increasing the signal-to-noise ratio). This may be a consequence of the fact that the MT neurons tuned to CM exhibit a broad range of direction-tuning bandwidths: between 32 and 186 deg [35]; these neurons can also respond to directions of motion that differ from the directions of the correlated dots. This reduces, by a constant amount, the probability that detector(s) tuned to correlated motion will respond to directions that are different from the optimal one (an outcome that is compatible with an increase in the response of GABAergic neurons by c-tDCS [35]). This would result in an increase in the signal-to-noise ratio, with the correlated motion activating a consequent sharpened tuning of the detector(s). In other words, a sharpening of the direction-tuning (caused by c-tDCS) would result in improved direction discrimination. Thus, the effect of tDCS can be explained by the local neuronal response to CM.

To explain the a-tDCS effect, a simple modulation of local, single-channel response is not comprehensive. Indeed, if a-tDCS increased the response of the neurons that were broadly tuned to the correlated motion, this would also increase both the coherent and incoherent signals, leaving a low signal-to-noise ratio. When explaining the a-tDCS effect, it might then be relevant to consider the evidence [33,34,36] that the estimated threshold may depend on the number of active detectors with different tuning functions. The task of selectively discriminating the direction of motion increases the activation of those neurons that are tuned to either correlated motion or the directions that moderately diverge from the test directions [33,37]. Jazayeri & Movshon [33] showed that left-right motion discrimination in a CM display relies mostly on the neurons that are tuned to correlated motion. Because of the system's internal noise, it is conceivable that, whereas some such detectors manifest above the threshold activation for target dots in a CM display, others do not reach the threshold. Thus, a-tDCS, by modulating (increasing) the probability of the firing rate, would activate more detectors tuned to correlated motion. In particular, even those that do not reach the threshold in the absence of stimulation may reach it as a consequence of a-tDCS stimulation. Hence, a-tDCS would increase the signal more than the noise, thus causing an increase in the signal-to-noise ratio, as reflected by a threshold reduction. Our results allow us to associate the tDCS effect to specific neural mechanisms that modulate the response of MT cells to CM: either pooling or increasing the tuning of the neurons that are responding to correlated motion. This accounts for the improved CM discrimination. Similar modulatory effects have been reported with the use of Transcranial Magnetic Stimulation (TMS) to target specific neural populations [38] and with low-intensity TMS, which has been shown to facilitate detection of relatively low CM; this result can be interpreted as an effect of stochastic resonance, through which the optimal level of noise pushes weak subthreshold signals across the threshold [39].

This result (in which tDCS has a selective effect for a stimulus presentation to the visual field that is contralateral to stimulation) is of methodological relevance, considering that interpretations based on sham-tDCS differences alone can be disputable. Indeed, researchers have found that participants sometimes can distinguish the real stimulation from the sham [40]. However, coupling the sham-tDCS difference with the result that occurred only with stimuli that were presented contralateral to the stimulation appears to both strengthen the evidence for a control-stimulation difference and eliminate the observer's expectation bias. We did not deliver tDCS to the right hemisphere, but we would have expected an effect on motion discrimination to the left hemifield. This is because a large number of studies have shown that left stimulation produces a greater modulation of the visual motion task than does right stimulation [41,42] and that TMS over the left MT produces more reliable [43] phosphenes than TMS over the right MT, thus indicating that the left area is more responsive when stimulated than the right.

With both c-tDCS and a-tDCS, participants showed better performance on Day 2, suggesting a PL effect. Specific analysis of the PL revealed a cross-day (late-PL) effect on the threshold (in agreement with previous results [44]) and an increase in the slope of the linear fitting of *d'*. These results indicate that late-PL works similarly to a-tDCS, with both producing a signal enhancement.

In conclusion, our evidence regarding the possible mechanisms underlying CM modulation by electrical stimulation could have relevant clinical implications, as CM has been shown to play a crucial role in both the diagnosis and the rehabilitation of visual disorders during the life span [45–47].

Conflict of interest

The authors declare that they have no competing financial interests.

Acknowledgments

Clara Casco received funding for this study from the University of Padova. We would like to thank Adel Ferrari for helping with data collection.

References

[1] Bindman LJ, Lippold OC, Milne AR. Prolonged changes in excitability of pyramidal tract neurones in the cat: a post-synaptic mechanism. J Physiol 1979;286:457–77.

[2] Creutzfeldt OD, Fromm GH, Kapp H. Influence of transcortical dc currents on cortical neuronal activity. Exp Neurol 1962;5:436–52.

[3] Nitsche MA, et al. Transcranial direct current stimulation: state of the art 2008. Brain Stimul 2008;1:206–23.

[4] Fritsch B, et al. Direct current stimulation promotes BDNF-dependent synaptic plasticity: potential implications for motor learning. Neuron 2010;66:198–204.

[5] Funke K. Quite simple at first glance–complex at a second: modulating neuronal activity by tDCS. J Physiol 2013;591. 3809–09.

[6] Bestmann S, de Berker AO, Bonaiuto J. Understanding the behavioural consequences of noninvasive brain stimulation. Trends Cogn Sci 2015;19:13–20.

[7] Antal A, Nitsche MA, Paulus W. External modulation of visual perception in humans. Neuroreport 2001;12:3553–5.

[8] Antal A, Kincses TZ, Nitsche MA, Paulus W. Manipulation of phosphene thresholds by transcranial direct current stimulation in man. Exp Brain Res 2003;150:375–8.

[9] Antal A, Kincses TZ, Nitsche MA, Paulus W. Modulation of moving phosphene thresholds by transcranial direct current stimulation of V1 in human. Neuropsychologia 2003;41:1802–7.

[10] Reinhart RM, Xiao W, McClenahan LJ, Woodman GF. Electrical stimulation of visual cortex can immediately improve spatial vision. Curr Biol 2016;26:1867–72.

[11] Antal A, et al. Direct current stimulation over V5 enhances visuomotor coordination by improving motion perception in humans. J Cogn Neurosci 2004;16:521–7.

[12] Accornero N, Voti PL, La Riccia M, Gregori B. Visual evoked potentials modulation during direct current cortical polarization. Exp Brain Res 2007;178:261–6.

[13] Antal A, Kincses TZ, Nitsche MA, Bartfai O, Paulus W. Excitability changes induced in the human primary visual cortex by transcranial direct current stimulation: direct electrophysiological evidence. IOVS 2004;45:702–7.

[14] Spiegel DP, Hansen BC, Byblow WD, Thompson B. Anodal transcranial direct current stimulation reduces psychophysically measured surround suppression in the human visual cortex. PLoS One 2012;7:e36220.

[15] Miniussi C, Harris JA, Ruzzoli M. Modelling non-invasive brain stimulation in cognitive neuroscience. Neurosci Bio Rev 2013;37:1702–12.

[16] Narasimhan S, Giaschi D. The effect of dot speed and density on the development of global motion perception. Vis Res 2012;62:102–7.

[17] Britten KH, Shadlen MN, Newsome WT, Movshon JA. The analysis of visual motion: a comparison of neuronal and psychophysical performance. J Neurosci 1992;12:4745–65.

[18] Britten KH, Shadlen MN, Newsome WT, Movshon JA. Responses of neurons in macaque MT to stochastic motion signals. Vis Neurosci 1993;10:1157–69.

[19] Salzman CD, Murasugi CM, Britten KH, Newsome WT. Microstimulation in visual area MT: effects on direction discrimination performance. J Neurosci 1992;12:2331–55.

[20] Cameron EL, Tai JC, Carrasco M. Covert attention affects the psychometric function of contrast sensitivity. Vis Res 2002;42:949–67.

[21] Prins N, Kingdom FAA. Palamedes: Matlab routines for analyzing psychophysical data. 2009.

[22] Ulrich R, Miller J. Threshold estimation in two-alternative forced-choice (2AFC) tasks: the Spearman-Kärber method. Percep Psychophy 2004;66:517–33.

[23] Macmillan NA, Creelman CD. Detection theory: a user's guide lawrence erlbaum associates. 2005. New York.

[24] Brainard DH. The psychophysics toolbox. Spat Vis 1997;10:433–6.

[25] Kleiner M, et al. What's new in Psychtoolbox-3. Perception 2007;36(1).

[26] Pelli DG. The VideoToolbox software for visual psychophysics: transforming numbers into movies. Spat Vis 1997;10:437–42.

[27] Pilly PK, Seitz AR. What a difference a parameter makes: a psychophysical comparison of random dot motion algorithms. Vis Res 2009;49:1599–612.

[28] Pavan A, Langgartner D, Greenlee MW. Visual short-term memory for global motion revealed by directional and speed-tuned masking. Neuropsychologia 2013;51:809–17.

[29] Martinez-Trujillo JC, Treue S. Feature-based attention increases the selectivity of population responses in primate visual cortex. Curr Biol 2004;14:744–51.

[30] Wright RD, Ward LM. Orienting of attention. Oxford University Press; 2008.

[31] Antal A, Nitsche MA, Paulus W. Transcranial direct current stimulation and the visual cortex. Brain Res Bull 2006;68:459–63.

[32] Fertonani A, Pirulli C, Miniussi C. Random noise stimulation improves neuroplasticity in perceptual learning. J Neurosci 2011;31:15416–23.

[33] Jazayeri M, Movshon JA. Integration of sensory evidence in motion discrimination. J Vis 2007;7:1–7.

[34] Cohen MR, Newsome WT. Estimates of the contribution of single neurons to perception depend on timescale and noise correlation. J Neurosci 2009;29:6635–48.

[35] Albright TD. Direction and orientation selectivity of neurons in visual area MT of the macaque. J Neurophysiol 1984;52:1106–30.

[36] Britten KH, Newsome WT, Shadlen MN, Celebrini S, Movshon JA. A relationship between behavioral choice and the visual responses of neurons in macaque MT. Vis Neurosci 1996;13. 87–00.

[37] Hol K, Treue S. Different populations of neurons contribute to the detection and discrimination of visual motion. Vis Res 2001;41:685–9.

[38] Silvanto J, Muggleton NG. Testing the validity of the TMS state-dependency approach: targeting functionally distinct motion-selective neural populations in visual areas V1/V2 and V5/MT+. NeuroImage 2008;40:1841–8.

[39] Schwarzkopf DS, Silvanto J, Rees G. Stochastic resonance effects reveal the neural mechanisms of transcranial magnetic stimulation. J Neurosci 2011;31:3143–7.

[40] Brunoni AR, et al. A systematic review on reporting and assessment of adverse effects associated with transcranial direct current stimulation. Int J Neuropsychopharmacol 2011;14:1133–45.

[41] Antal A, et al. Facilitation of visuo-motor learning by transcranial direct current stimulation of the motor and extrastriate visual areas in humans. Eur J Neurosci 2004;19:2888–92.

[42] Hotson J, Braun D, Herzberg W, Boman D. Transcranial magnetic stimulation of extrastriate cortex degrades human motion direction discrimination. Vis Res 1994;34:2115–23.

[43] Silvanto J, Lavie N, Walsh V. Double dissociation of V1 and V5/MT activity in visual awareness. Cereb Cortex 2005;15:1736–41.

[44] Ball K, Sekuler R. Direction-specific improvement in motion discrimination. Vis Res 1987;27:953–65.

[45] Grinter EJ, Maybery MT, Badcock DR. Vision in developmental disorders: is there a dorsal stream deficit? Brain Res Bull 2010;82:147–60.

[46] Billino J, Bremmer F, Gegenfurtner KR. Differential aging of motion processing mechanisms: evidence against general perceptual decline. Vis Res 2008;48:1254–61.

[47] Huxlin KR, et al. Perceptual relearning of complex visual motion after V1 damage in humans. J Neurosci 2009;29:3981–91.