Evidence of top-down modulation of the Brentano illusion but not of the Glare effect by transcranial Direct Current Stimulation

Ottavia Maddaluno[1], Alessio Facchin[1,2,3], Daniele Zavagno[1,2], Nadia Bolognini[1,4], Elisa Gianoli[1], Elisa Maria Curreri[1], Roberta Daini[1,2]

[1] Department of Psychology, and Milan Center for Neuroscience (NeuroMI), University of Milano-Bicocca, Milano, Italy;

[2] University research centre in optics and optometry, University of Milano-Bicocca (COMiB), Milano, Italy;

[3] Institute of Research and Studies in Optics and Optometry, Vinci, Italy

[4] Neuropsychological Laboratory, IRCCS Istituto Auxologico Italiano, Milano, Italy

Corresponding Author:
Ottavia Maddaluno
Department of Psychology - University of Milano-Bicocca
Piazza dell'Ateneo Nuovo 1
20126, Milano, Italy
Email o.maddaluno@campus.unimib.it

Abstract:

Transcranial Direct Current Stimulation (tDCS) has been widely used for modulating sensory, motor and cognitive functions, but there are only few attempts to induce and change illusory perception. Visual illusions have been the most traditional and effective way to investigate visual processing through the comparison between physical reality and subjective reports. Here we used tDCS to modulate two different visual illusions, namely the Brentano illusion and the Glare effect, with the aim of uncovering the influence of top-down mechanisms on bottom-up visual perception in two experiments. In experiment 1, to a first group of subjects, real and sham cathodal tDCS (2 mA, 10 min) were applied over the left and right posterior parietal cortices (PPC). In experiment 2, real and sham cathodal tDCS were applied to the left and right occipital cortices (OC) to a second group of participants. Results showed that tDCS was effective in modulating only the Brentano illusion, but not the Glare Effect. tDCS increased the Brentano illusion but specifically for the stimulated cortical area (right PPC), illusion direction (leftward), visual hemispace (left), and illusion length (160 mm). These findings suggest the existence of an inhibitory modulation of top-down mechanisms on bottom-up visual processing specifically for the Brentano illusion, but not for the Glare Effect. **The lack of effect of occipital tDCS should consider the possible role of ocular compensation or of the unstimulated hemisphere, which deserve further investigations.**

Keywords:

Visual illusions, brightness, transcranial direct current stimulation, top-down modulation.

Introduction

Visual illusions have been used to investigate the properties of the visual perceptual system (Coren and Girgus 1978). One main assumption is that visual illusions are mere perceptual bottom–up phenomena, arising from the low-level information processing in the brain. There are two sets of evidences that support such view. On one hand, some neuropsychological studies suggest that in presence of a brain damage to high-order visual and spatial cortical areas, the processing of illusions are preserved (Mattingley et al. 1995; Vallar et al. 2000; Daini et al. 2002). On the other hand, neuroimaging studies found that visual illusions induce the activation of brain areas involved in lower-order processes (Hirsch et al. 1995; Ffytche and Zeki 1996; Larsson et al. 1999; Mendola et al. 1999).

Of particular interest are studies on brain-damaged patients with unilateral spatial neglect (USN). The USN is a neuropsychological syndrome in which patients fail to orient, respond or move to stimuli presented in the contralesional side of space (Heilman and Valenstein 1979; Vallar 1998; Vallar and Bolognini 2014). However, in USN patients the processing of visual illusions of length perception – such as the Müller-Lyer illusion, or its version known as the Brentano illusion (Fig. 1A) – is not only preserved but also expanded in the contralesional side of space (Mattingley et al. 1995; Vallar et al. 2000; Vallar and Daini 2002). In particular, Vallar and collaborators (2000) examined USN patients and healthy controls in a bisection task with the Brentano illusion. They found that the performance of both groups was similarly influenced by the orientation of the illusion, highlighting that the illusory effects were not merely present in USN patients, but even enlarged. Subsequently, Daini and collaborators (2002) investigated the spatial and visual processing of the Brentano illusion comparing the performance of USN patients with and without hemianopia (H+, H-), a central visual field defect consisting in the loss of vision in the half-field contralateral to a post-chiasmal lesion. The results of this study showed that H+ USN patients did not perceive the leftward Brentano illusion, while H- USN patients did, and they also showed an enlarged effect despite the lack of conscious perception to that side of space.

Unilateral spatial neglect comes from lesions involving different brain areas: frontal (Husain et al. 1997; Karnath et al. 2004), parietal (Vallar 2001; Vallar et al. 2003), temporal (Karnath et al. 2001; Golay et al. 2008), and subcortical (Healton et al. 1982; Karnath et al. 2002). On the contrary, hemianopic patients present low-level visual field defects that arise from damage to the occipital cortex and related white matter tracts (Verdon et al. 2009).

Another piece of evidence comes from a fMRI study by Weidner and Fink (2007), in which healthy subjects were asked to judge pre-bisected lines, with and without Brentano illusion configurations that differed in magnitude. This type of task has clearly a visuospatial component, which is the judgment of the correct midpoint of the line. In accordance with the neuropsychological literature, the spatial judgment activated the right posterior parietal cortex and the right temporo-occipital cortex, while the magnitude of the illusory effect was mediated by both occipital cortices and the right superior parietal cortex (Weidner and Fink 2007).

These results, taken together, suggest the involvement of both visuo-spatial mechanisms mediated by parietal areas, and bottom-up sensory processing that arises from primary visual areas in the occipital cortex. Thus, our first hypothesis was that the mechanisms underlying the Brentano illusion could be mediated by parietal and occipital areas.

In the present study we took into consideration also another phenomenon that pertains a different class of visual illusions: the Glare effect. This is a brightness illusion in which – in its canonical cross-like configuration – a white square target appears to glow or even self-luminous when flanked on all four sides by squares made of luminance gradients ranging from black outwards to white inwards (Zavagno 1999; Zavagno and Caputo 2005; Zavagno and Daneyko 2017). In our context this illusion is interesting because its underlying mechanisms (luminosity perception) should be quite different from the Brentano illusion. Nevertheless, even for the Glare effect there is some evidence that the illusion arises from primary visual areas (Leonards et al. 2005; Lu et al. 2006).

Recently, with the use of non-invasive transcranial brain stimulation (NIBS) techniques, it has become possible to interfere with the activity of specific brain areas, inducing reversible and transient changes in the neuronal excitability (Rossi et al., 2009; Woods et al., 2016). Transcranial Direct Current Stimulation (tDCS) is one of such technique, which allows to modulate the functionality and plasticity of the central nervous system by means of low amplitude direct current passing through the skull. The low current intensity applied to the skull is safe but sufficient to modify the transmembrane neuronal potential (Giglia et al. 2011), thus affecting cortical excitability by modulating neuronal firing rates (Nitsche et al. 2003; Zaghi et al. 2010). tDCS does not produce directly action potentials, but it polarizes brain tissues in two ways: anodal stimulation is thought to increase cortical excitability, while cathodal stimulation seems to reduce excitability.

In the last decades, tDCS has been usefully applied to investigate the neural basis of different mental processes, among which visual perception and visuo-spatial attention. Some studies using tDCS, for instance, have mimicked neglect-like behavior on healthy subjects. In particular, Giglia et al. (2011) showed that "dual" stimulation (cathode over the right hemisphere and anode over the left one) of both parietal cortices produced a rightward bias in the symmetry judgment of pre-bisected lines.

Taking into account all previous observations, we aimed at investigating whether and how the Brentano illusion and the Glare effect could be modulated by tDCS. In particular, in two independent experiments we tested the effects of tDCS over two different brain areas (i.e. parietal and occipital cortices). In experiment 1 we assessed the effect of unilateral posterior parietal stimulation on the illusions; parietal tDCS would likely affect attentional processes, in turn amplifying the illusory effect; experiment 2 investigated – in a different group of participants - whether unilateral occipital stimulation could interfere with the perception of visual illusions by inducing an alteration. We expected that the parietal stimulation would cause an enhancement of the Brentano illusion by interfering with the attentional resizing of the inducers effect, as suggested by the results on neglect patients without hemianopia (Daini et al. 2002). Furthermore, we expected to find an alteration of the illusory effects by interfering with the occipital processing because of the role of these areas in building the percepts. Previous studies with hemianopic patients (Daini et al.

2002) showed that these can perceive the Brentano illusion, and that the unaffected occipital hemisphere can supply for the lack of processing of the other one.

We wondered whether also the Glare effect would show changes in its appearance, and thus whether the modulations would be generalizable across different types of visual illusory phenomena. The Brentano illusion and the Glare effect, in fact, belong to different classes of illusions, the first is an optical-geometric illusion, the second a brightness illusion. Both, however, occur in relation to how geometric information is displayed and attended to.

Methods

Experiment 1 – Posterior parietal cortex

Participants

First of all, we performed a power analysis in order to calculate the minimum sample size required to obtain a significant result. Using the 80% power for detecting a small size effect with an alpha criterion of statistical significance of 0.05 and the planned structure of analysis, we estimated that at least 31 participants in each group were necessary.

Thirty-three healthy participants took part to experiment 1 (mean age ± SD, 23±3; 13 males). All participants were right handed on a standard questionnaire (Oldfield 1971) and had normal or corrected to normal vision. All participants gave their informed consent prior to being involved in the study. The experiment was carried out according to the ethical standards of the Declaration of Helsinki and was approved by the local Ethics Committee of Milano-Bicocca University (Protocol number 248). None of the participants reported a history of: neurological or psychiatric disorders, epileptic seizures, intracranial metallic implants, cardiac diseases, substance abuse or dependence. These criteria met the safety guidelines for the use of non-invasive brain techniques (Nitsche et al. 2003; Rossi et al. 2009; Rossini et al. 2015).

Stimuli and procedure

Brentano's version of the Müller-Lyer illusion was used (Coren and Girgus 1978). The Brentano stimuli consisted in a red line with black fins at the center and extremities. Stimuli were printed on A4 sheets (Facchin et al., submitted). The task comprised three kinds of stimuli: leftward illusion (left-sided outgoing fin/right-sided ingoing fin), line (no fins) and rightward illusion (left-sided ingoing fishtail/right-sided outgoing fishtail) (see Figure 1). Red lines came in two lengths, 80 and 160 mm. The fins were 20 mm long for 80 mm lines and 40 mm long for 160 mm lines. The width of the lines in all configurations was 2 mm. The fins formed a 45° (ingoing) or a 135° (outgoing) angle with the line.

Stimuli were presented in a random fixed order on paper with a spiral notebook. Each stimulus was presented 5 times for a total number of 30 presentations (for details see Facchin et al., submitted).

The spiral notebook was aligned with the mid-sagittal plane of the participant's trunk. Participants were required to mark the midpoint of the red line with a soft marker pen. They were instructed to mark as fast as possible the midpoint using their right hand; after each trial they were requested to place the hand in the starting position. Deviations from the objective midpoint of the red line were measured to the nearest millimeter. A positive score denoted a rightward bias, a negative score a leftward bias.

The Glare Effect illusion consists of 4 squares shaded with a quasi-linear luminance ramp arranged around a white central square, drawn on a white background. This configuration gives rise to an impression of self-luminosity of the central square. It is possible to vary the intensity of the brightness illusion by modifying the luminance range of the squares' ramps around the central white square (Zavagno 1999).

To test the Glare effect, we used the Glare Effect Test (Facchin et al. 2017), that consists in 101 12 x 12 cm plastic cards in which reflectance ramps of the Glare Effect figure (10.5 x 10.5 cm) change gradually from solid black (card 0) to full black-to-white (card 101) in smooth steps. We employed a two-alternative forced choice task (2AFC), which we simplified by using only half of the deck (49 cards plus the 2 reference cards). Before the experiment started, participants received instructions about the experimental task. The examiner placed the two reference cards on a table at a distance of 40 cm from the participant's eyes and showed the experimental cards in random order, one at a time. Participants were first asked how the central square of the two reference cards differed. Then, using some of the unused cards from the deck as examples, participants were asked to indicate for each example card to which reference card the central square appeared more similar. In conducting this trial task, participants were instructed to focus only on the appearance of the central square. Once the participant understood the task, s/he was engaged in the 2AFC task with all 49 experimental cards.

Glare effect responses to stimuli were recorded as follow: a score of zero was assigned to cards categorized as similar to reference card 0, while cards perceived similar to reference card 101 were assigned a score of 1. Afterward the data were ordered by card number and fitted with a psychometric function using R (R Core Team 2017). A logistic regression model (logit) for each participant and session was calculated in order to extract a Point of Subjective Equivalence (PSE) and to obtain the slope of the function. PSE represents a score of Glare Effect magnitude; zero denotes the absence of Glare Effect and 99 the maximum effect. The slope of regression represents the precision of the estimation. The procedure is identical to the one used in the definition of the Glare Effect Test, only adapted to 49 cards (Facchin et al., 2017). To ascertain the goodness of fit of the regression, the Hosmer-Lemeshow test was applied for each participant and session (Hosmer, Lemeshow & Sturdivant 2013). A visual inspection of data together with the fitted curve was also performed to exclude extreme performances and/or inaccurate estimations (e.g. estimations that appear to be random).

The order of presentation of the two illusions was counterbalanced among participants.

Neuromodulation

Participants underwent the two visual illusions, Brentano and Glare effect, while receiving online cathodal tDCS, to the left and right posterior parietal cortex (PPC), or sham stimulation for a total of three sessions. The order of administration (Sham, left PPC, right PPC) was randomized and balanced between participants. tDCS was delivered by a battery-driven constant current stimulator (BrainStim, EMS, http://brainstim.it), using a pair of surface saline-soaked sponge electrodes. For *real* stimulation the polarity was cathodal (2mA/35 cm^2). The current was ramped up over 10 s, held constant at 2mA for 10 minutes and then ramped down over 10 s. The positions of the targeted areas were chosen according to the 10-20 system for EEG electrode placement. The active electrode was placed over P3 or P4, two locations that overlie PPC of the right and the left hemisphere, respectively. The reference electrode was placed over the contralateral supraorbital area. This montage has proven to be effective in previous studies (Nitsche et al. 2008; Boggio et al. 2009). TDCS (duration= 10 min) was delivered online, during the tasks, starting the stimulation 3 minutes before the beginning of the experimental tasks (together, the 2 tasks lasted about 7 min, see Figure 1). This duration of stimulation was sufficient to have an effect over cortical excitability, outlasting the entire duration of the tasks (Nitsche and Paulus 2001). For sham stimulation, the current was ramped over 30 s and then quickly turned off. This procedure is known to give exactly the same tingling sensation to participants, but it has no effects on brain polarization (Gandiga et al. 2006). During the sham tDCS, the electrodes arrangement was the same as in the real stimulation.

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Results

Brentano Illusion

In order to evaluate the effect of tDCS in modulating the length illusion, we calculated the illusory effect by subtracting the bisection error of the simple lines from the bisection error of the illusory stimuli. In this way we obtained two variables: the rightward illusory effect and the leftward illusory effect. In order to make the two different illusion effects more comparable we reversed the leftward illusion effect by multiplying it by -1. Furthermore, here we report sensitivity to Brentano illusion (mean = 6%, S.D. =3%, range =1-14%) calculated on the data collected during sham sessions (considered as a baseline). Before running the analyses, the sphericity requirements for the repeated measures ANOVAs were assessed by using Mauchly's test for each data set. Where the assumptions were not met, the Greenhouse–Geisser correction was used for the violations of sphericity.

We then performed a repeated-measures (3X2X2) analysis of variance (ANOVA) with three within-subjects factors: tDCS Session (Sham, left PPC, right PPC), Length (80 mm and 160 mm) and Direction (rightward and leftward illusion). Results showed a significant main effect of Length (F1,32 = 50.77, p <.001, η2p= 0.61) and Direction (F1,32 = 14.06, p<.001, η2p= 0.31). Moreover, results highlighted a significant interaction Direction X Session (F2,64 = 3.80, p <.05, η2p= 0.11). No other significant effects were found (Session: F2,64=1.11, p=0.34; Length X Direction: F1,32=3.68, p=0.06; Length X Session: F2,64=1.17, p=0.32; Length X Direction X Session: F2,64=0.66, p=0.49). The significant Direction X Session interaction was further explored by running separate analyses for each illusory effect. Furthermore, Figure 2 shows that the size of the illusion in the two directions is undoubtedly different, so we subsequently compared the illusory effects separately, based on the direction of the illusions (i.e. rightward vs leftward illusion).

We performed a repeated-measures (3X2) analysis of variance (ANOVA) with two within-subjects factors: tDCS Session (Sham, left PPC, right PPC) and Length (80 mm and 160 mm) for each direction of the illusion. Regarding the rightward illusion, results showed a significant effect of the main factor Length ($F_{1,32}$=24.72, p<0.001, η^2_p=0.44). No significant effects were found for the stimulation conditions or the interaction between stimuli length and sessions: Session ($F_{2,64}$=0.97, p=0.37), Session X Length ($F_{2,64}$=0.05, p=0.96).

On the other hand, analysis on the leftward illusion showed a significant effect of the main factor Session ($F_{2,64}$=3.99, p<0.05, η^2_p=0.11) (See Figure 2). Post hoc analysis with Bonferroni correction, revealed a significant increase of the illusory effects following the real tDCS over the right PPC only, as compared to the sham tDCS (t_{64}=2.54, p=0.048).

Furthermore, the main effect of Length was also significant ($F_{1,32}$=6.00, p<0.05, η^2_p=0.16). No other significant effects were found: Session X Length ($F_{2,64}$=1.50, p=0.23).

---------------------------------- Figure 2 about here------------------------------------

Glare Effect

All participants and sessions passed the Hosmer-Lemeshow test for goodness of fit, nevertheless visual inspection of data and regression curves showed that one participant had a too gentle slope as a sign of inaccurate estimation and was excluded from the analysis.

Statistical analyses were performed separately for PSEs and slopes. A repeated-measures ANOVA with the within-subjects factor tDCS Session (sham, left PPC, right PPC) was conducted to assess changes in PSEs according to different conditions of stimulation. No significant differences across the stimulation conditions were found (F2,62=0.76, p=0.47). The same analysis was conducted on slopes and no significant effects were found (F2,62=1.15, p=0.32). The results are plotted in Figure 3.

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Experiment 2 – Occipital cortex

Participants

Thirty-three participants (mean age ± SD, 23±2; 10 males), different from Experiment 1, were recruited using the same criteria as described for Experiment 1.

Stimuli, procedure and neuromodulation

The same experimental tasks and procedure of Experiment 1 was used, except for the position of the electrodes, which for sham or real cathodal tDCS (2mA/35 cm^2) were placed over the left or right occipital cortex (OC). During real stimulation the active electrode was placed, according to the 10/20 EEG system, over O1 or O2, two locations overlying the primary occipital cortex (V1) of the right and the left hemisphere, respectively. The reference electrode was placed over Cz, according to evidences of previous studies, indicating that this is the optimal electrode arrangement to achieve current-driven cerebral excitability changes in OC (Antal, et al., 2004; Bolognini et al., 2011).

Results

Brentano Illusion

We adopted the same statistical approach used for Experiment 1, namely a 3x2x2 repeated-measures ANOVA, with three within-subjects factors: tDCS Session (Sham, left OC, right OC), Length (80 mm and 160 mm) and Direction (rightward and leftward illusion). We found a significant main effect of Length (F1,32=39.24, p<.001, ηp2=0.55) and Direction (F1,32=12.17, p<.01, ηp2=0.28). No differences across tDCS conditions were found, showing that occipital stimulation did not modulate the illusion: Session (F2,64=0.94, p=0.40). No significant interaction was found: Length X Direction (F1,32=2.70, p=0.11), Length X Session (F2,64=1.27, p=0.29), Direction X Session (F2,64=0.12, p=0.88), Length X Direction X Session (F2,64=2.84, p=0.07). Results are shown in Figure 4. Sensitivity to the Brentano illusion: mean= 7%, S.D. = 4%, range =-1- 21%.

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Glare Effect

Only two subjects and only in one condition did not pass the Hosmer-Lemeshow test for goodness of fit, for this reason we decided not to discard them. However visual inspection of data and regression curves showed that another participant had a too gentle slope, a sign of inaccurate estimation, while another one showed a steeper estimation with extreme values. Consequently, the data from these two participants were excluded from the analysis.

A repeated measures ANOVA, with tDCS Session (Sham, left OC, right OC) as within-subjects factor, was conducted to assess changes in PSEs according to different conditions of stimulation. No significant differences across the stimulation conditions were found ($F_{2,60}=0.19$, $p=0.83$). The same kind of analysis was conducted on slopes and we found no significant effects ($F_{2,60}=0.81$, $p=0.45$). Results are shown in Figure 5.

---------------------------------- Figure 5 about here-----------------------------------

Discussion

The aim of this study was to explore the possibility of modulating visual illusions, such as the Brentano Illusion and Glare effect, by modulating excitability in cortical areas involved in top-down attentional (PPC, Experiment 1) and bottom-up (OC, Experiment 2) visual processing. In particular, cathodal tDCS was delivered over two cortical areas likely involved in the emergence and the resizing of the two illusory phenomena, although in different stages of processing: PPC and OC of both the left and right hemisphere.

Overall results showed that tDCS increases the Brentano illusory effect, but not the Glare illusory effect. The modulation of PPC modified the perception of the Brentano illusion with an enlargement of the illusory effect. Furthermore, this effect is specific for the right hemisphere stimulation, which brings selectively to increase the leftward bisection bias, mimicking the performance of USN patients.

Brentano illusion

Our first hypothesis was based on the modulation in the perception of the Brentano illusion after different brain lesions: parietal and occipital cortical damages due to stroke, lead to different alterations of the illusory phenomenon, as well as to different behavioral impairments, namely USN and hemianopia. The presence of homonymous hemianopia, after an OC lesion, affects the bottom-up processing of illusory phenomena when no exploration of the whole figure is possible. Accordingly, Daini et al (2002) found that patients affected by homonymous hemianopia (confirmed by visual evoked potentials) and USN do not direct eyes-movements toward the contralesional (blind/neglected) hemifield because they are not conscious of that side of space. However, in the chronic stage of illness, hemianopic patients without USN may spontaneously develop compensatory oculomotor exploration to compensate for the visual field loss (Machner et al. 2009), which in turn may favor the perception of the illusion (Daini et al., 2002). In this perspective, a possible speculation is that healthy individuals after unilateral tDCS over OC might perform compensatory eye movements in a similar way of hemianopic patients and do not show significant effects. Conversely, the presence of USN may alter differently the perception of this illusion: right brain damaged patients with USN perceive the illusion asymmetrically, with leftward side of the illusion expanded compared to the right side.

In our study, neurologically healthy participants showed an increased leftward bias in the Brentano illusion after cathodal tDCS of the PPC. We found that tDCS effects were illusory configuration- and hemisphere-specific: only tDCS over the right, but not left, PPC induces a specific modulation selectively on the leftward Brentano illusion. These findings are consistent with previous studies with brain-damaged patients. Daini et al. (2002) demonstrated that in patients with left USN, without hemianopia, and a lesion affecting the right PPC, the illusory effect was not only present but even larger in the neglected, contralesional, side of space. Our result with tDCS overlaps such findings, suggesting that the illusory effect underlying the Brentano illusion is modulated by the right PPC. Either electrical stimulation or brain lesion of PPC, indeed, interfere with visuo-spatial attention (Vallar 2001; Vallar et al. 2003). These findings suggest a top-down modulation on the bottom-up visual processing of the illusion of length. Previous neuroimaging studies suggested an involvement of parietal cortices in a similar visuo-spatial illusion (Weidner and Fink 2007); our finding provide a direct evidence in healthy individuals of the role of PPC as the neural substrate of this inhibitory top-down processing in this illusion of length.

Furthermore, we found that the illusory effect was stronger for longer stimuli (i.e. 160 mm stimuli). This is consistent with previous studies showing that the bisection error, as much as the sensitivity to visual illusions, increases with the length of the line (Restle and Decker 1977; Vallar et al. 2000). Studies with USN patients with hemianopia suggest that direct processing of the Brentano illusion arises from the primary visual cortex (OC). In fact, lesions involving posterior cortical regions disrupt the illusion’s perception. Daini and colleagues (2002), proposed that hemianopic patients without USN show a preserved illusory effect as due to preserved eye movements (Ishiai et al. 1987; Kerkhoff and Schenk 2011) and to a strategic compensation of the lack of unilateral visual input (Zihl, 1995).

In our results, unilateral occipital tDCS had no effect in modulating the illusion. One possible explanation could be that, even if we have successfully interfered with occipital brain activity, participants could still explore the whole stimuli with eye movements, in turn perceiving the entire stimulus within the contralateral (with respect to the tDCS side) visual hemifield and consequently performing normally on this task. Nevertheless, future studies with computer presentations and eye movement recordings should be run to verify this hypothesis. Another possibility is that the illusory perception brought about by the Brentano illusion relies more strongly on the activity of extra-striate and parietal areas, rather than being a by-product of primary visual areas. In both cases, we found convergent results from brain lesion and brain neuromodulation (by cathodal tDCS): 1) either hemianopia or unilateral occipital tDCS resulted in the same full sensitivity to the illusory configuration, 2) the unilateral right parietal tDCS mimics the effect of the left USN caused by a PPC lesion. In order to test whether our tDCS parameters and target areas affect visual illusions in general, we tested the efficacy of the same stimulation on the Glare effect, a brightness illusion that has little in common with the Brentano illusion.

Glare effect illusion

We used the Glare Effect Test (Facchin et al. 2017) as a tool to investigate the modulation of an illusory perception along a different visual dimension, i.e. luminosity.

In recent studies by Bolognini et al. (2011), tDCS has been proven to be an effective tool to modulate illusory perceptual phenomena, within and across sensory modalities. In the visual domain, for instance, Scocchia et al. (2015) showed how cathodal tDCS of the occipital cortex (OC) can affect the perception of movement in the “two-third power law” illusion, increasing individual sensitivity to the illusory motion.

Differently, in this case the same tDCS protocols used to modulate the Brentano illusion did not affect the sensitivity to the Glare effect. Not only we did not find any effect when unilateral cathodal tDCS was applied over OC, which was also ineffective on the Brentano illusion, but we did not find any effect when the unilateral stimulation was applied over PPC of both hemispheres. There are several possible explanations for these results.

Firstly, as much as the Brentano illusion, the unilateral tDCS that interferes with the activity of V1 of one hemisphere leaves the homologue area in the other hemisphere able to compensate for it. We can presume that a similar effect could be found in hemianopic patients with unilateral brain lesions.

Secondly, as animal and human studies seem to suggest (Rossi et al. 1996; MacEvoy and Paradiso 2001; Haynes et al. 2004; Leonards et al. 2005; Boyaci et al. 2007), the neural substrates of brightness contrast and lightness seem to involve a neural network which include striate and extra striate cortices, but also subcortical areas as the lateral geniculate nucleus (Rossi & Paradiso, 1999). Due to its technical properties, tDCS can only modulate the neuronal activity of the superficial layers of the cerebral cortex. Thus, the electric current cannot interfere with the subcortical activity of subcortical areas. On the other hand, electrophysiological studies showed that occipital tDCS effects are stimulus-dependent whereby an increase in stimulus contrast (here luminosity) may reduce or even wash away the effect of occipital tDCS (Antal et al. 2004). The hypothesis put forward is that whenever an external visual stimulus activates the OC maximally, the sub-threshold excitability shifts induced by tDCS may be physiologically irrelevant as for producing a clear change in the illusory perception (Vallar and Bolognini 2011).

Additionally, we did not find any changes in the sensitivity to Glare effect even following the parietal stimulation. It could be that the Glare effect, being a brightness illusion, is treated differently by the visual system, with less constraints as regards to the geometry of the illusion. In general terms, brightness as a perceptual outcome may rely on coarser mechanisms (Zavagno, Daneyko, and Sakurai, 2011). Such hypothesis is congruent with the recently advanced hypothesis of a specific neuronal circuit for pupil responses (Zavagno, Tommasi, and Laeng, 2017), in charge of controlling the amount of light entering the eye based on brightness maps of the visual scene rather than on absolute luminance. The purpose of such a circuit would to offer the correct amount of light in every situation. In view of these hypothesis, the lack of effects we observed with the Glare effect are not surprising. Indeed, with the Brentano illusion task, one is called to indicate the central point of a line, which requires precision and therefore attention; with the Glare effect test, instead, one is required to detect the presence of self-luminosity, which seems to rely on brightness maps. Finally, there is no evidence of an involvement of PPC in luminosity perception (Rossi and Paradiso 1999; MacEvoy and Paradiso 2001; Leonards et al. 2005). Our results, therefore, confirm that there is no involvement of parietal cortices in the generation of brightness illusions. It follows that the top-down modulation by parietal tDCS observed for Brentano illusion is, for what we know, illusion-specific; in this sense it would be interesting to test whether parietal tDCS affects other optical-geometrical illusions.

The present study has some limitations. As mentioned above, we did not directly verify the compensatory role of eye movements in unilateral occipital stimulation, hence future studies providing an empirical assessment of eye movements (e.g. eye tracker) could further confirm or disconfirm this hypothesis.

Another point regards the mechanism underlying the influence of tDCS over illusory phenomena. Future research investigations employing other non-invasive brain techniques (such as Transcranial Magnetic Stimulation, TMS, and transcranial alternating current stimulation, tACS) could help to clarify these mechanisms. For example, recent studies successfully employed tACS to investigate the involvement of certain types of oscillatory frequencies in the alternation of conscious percept of bistable figures (Strüber, Rach, Trautmann-Lengsfeld, Engel, and Herrmann, 2014; Cabral-Calderin, Schmidt-Samoa, and Wilke, 2015), suggesting that this could be an interesting methodology to further investigate modulatory effects on illusory perception

Conclusions

This is one of the few studies using tDCS applied to study the illusory perception (Scocchia et al., 2015; see also Bolognini et al., 2011; Marques et al., 2014; Convento et al., 2018 for crossmodal illusion). Here we successfully modulated the processing of Brentano illusion using electrical stimulation. In line with evidence from studies with brain-damaged patients, cathodal tDCS of the

PPC enhances the Brentano illusion illusory effect. Furthermore, our findings suggest the presence of a hemispheric asymmetry in modulating the illusion of length. In fact, only the stimulation of the right posterior parietal cortex increased the illusion. Taken together, this evidence suggests the presence of a right parietal top-down modulation on the bottom-up visual processing at the basis of the Brentano illusion.

On the contrary, the modulation induced by cathodal tDCS did not affect the Glare effect, a brightness illusion. This means that the effects of cathodal tDCS are not generalizable to all visual illusions, but it opens to the hypothesis that such type of stimulation may affect the perception of a certain class of phenomena pertaining to the category of optical-geometric illusions. Finally, unilateral occipital stimulation did not modulate responses to the illusions.

Conflict of Interest Statement

The authors declare that they have no conflict of interest.

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Figure captions

Fig. 1 Temporal sketch of procedure of administration of tests and brain stimulation.

Fig. 2 Rightward (R) and leftward (L) illusory effect after placebo stimulation (sham), left posterior parietal cortex (left PPC) stimulation and right posterior parietal cortex (right PPC) stimulation. A) results for 80 mm stimuli, B) results for 160mm stimuli.

Fig. 3 Glare Effect magnitude (A) and precision of estimation (B) after left PPC, right PPC and sham stimulation. Bars represent +/1 SEM.

Fig. 4 Rightward (R) and leftward (L) illusory effect after placebo stimulation (sham), left occipital cortex stimulation (left OC) and right occipital cortex (right OC) stimulation. A) results for 80 mm stimuli, B) results for 160mm stimuli.

Fig. 5 Glare Effect magnitude (A) and precision of estimation (B) after left OC, right OC and sham stimulation. Bars represent +/1 SEM.