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I find you more attractive … after (prefrontal cortex) stimulation

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ABSTRACT

Facial attractiveness seems to be perceived immediately. Neuroimaging evidence suggests that the appraisal of facial attractiveness is mediated by a network of cortical and subcortical regions, mainly encompassing the reward circuit, but also including prefrontal cortices. The prefrontal cortex is involved in high-level processes, so how does its activity relate to beauty appreciation? To shed light on this, we asked male and female participants to evaluate the attractiveness of faces of the same and other sex prior and after transcranial direct current stimulation (tDCS) over the dorsolateral prefrontal cortex (DLPFC). We found that increasing excitability via anodal tDCS in the right but not in the left DLPFC increased perceived attractiveness of the faces, irrespective of the sex of the faces or the sex of the viewers. Identical stimulation over the same site did not affect estimation of other facial characteristics, such as age, thereby suggesting that the effects of anodal tDCS over the right DLPFC might be selective for facial attractiveness, and might not generalize to decisions concerning other facial attributes. Overall, our data suggest that the right DLPFC plays a *causal* role in explicit judgment of facial attractiveness. The mechanisms mediating such effect are discussed.

1. Introduction

Consistent evidence shows that there is a strong agreement across individuals belonging to different cultures and sexes (even from the very early development) about whether a face is attractive or not (e.g., Langlois et al., 2000). Cognitive and evolutionary psychologists have long debated about what makes a face attractive. Among the most common features, research has focused on facial averageness, symmetry, sexual dimorphism, and skin quality as possible relevant factors (for a review, see Rhodes, 2006). From an evolutionary perspective, these attributes may act as critical biological signals in mate selection, enhancing reproductive success (e.g., Perrett et al., 1994, 1998).

Studies investigating the neural correlates of facial attractiveness judgments converge in pointing to a network of cortical and subcortical areas including the orbitofrontal cortex, the nucleus accumbens, the ventral striatum, the amygdala, but also the lateral and medial prefrontal cortex bilaterally (e.g., Chatterjee et al., 2009; Cloutier et al., 2008; Kranz and Ishai, 2006; Martín-Loeches et al., 2014; O'Doherty et al., 2003; Vartanian et al., 2013; Winston et al., 2007; for meta-analyses, see Bzdok et al., 2011, and Mende-Siedlecki et al., 2013). The neural circuitry underlying appreciation of facial attractiveness shows a considerable (but not complete) overlap with brain regions involved in reward (such as the nucleus accumbens, amygdala, and orbitofrontal cortex). This overlap likely reflects the emotional responses elicited by attractive faces (cf. Aharon et al., 2001; Senior, 2003). Nonetheless, the evaluation of facial attractiveness may rely on two different processes engaged simultaneously. One process is related to activity throughout the reward circuit, especially in response to attractive faces of the preferred sex. In particular, attractive faces are rewarding in that they induce a conscious (or unconscious) experience of pleasure (see Berridge et al., 2009) possibly associated to mate choice. The other process is based on an aesthetic evaluation, not directly governed by appraisals of reward value (Aharon et al., 2001; Senior, 2003; see also Leder et al., 2004, for a more general discussion on other sources of aesthetic pleasure). Accordingly, certain areas of the reward circuit have been found to show

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enhanced responses selective for faces of the preferred sex, whereas other brain regions, including lateral sectors of the prefrontal cortex, respond to facial attractiveness to a similar extent regardless the sex of the face and the sex of the viewer (Kranz and Ishai, 2006).

Although the role of the reward system in the evaluation of facial attractiveness has been well characterized, the specific role of the prefrontal cortex remains less clear. The dorsolateral prefrontal cortex is known to mediate high-level processes (such as planning or problem solving), so what role can it play in appraisal of facial attractiveness? In an early PET study, Nakamura et al. (1998) found greater activity in the (left) prefrontal cortex during explicit attractiveness judgments compared to judgments of facial emotions or face-background colour, and concluded that prefrontal activations were probably due to additional requirements in the facial attractiveness rating task compared to merely processing facial features. Winston et al. (2007) reported significantly higher activation in the superior frontal gyrus during attractiveness compared to age judgments of the same faces, suggesting a greater involvement of the DLPFC in aesthetic evaluation than in decisions about other facial attributes. More recently, Chatterjee et al. (2009) showed that activity in the DLPFC observed during attractiveness explicit rating (but not during a face-identity judgment task) reflected attention and decision-making components of the task. Furthermore, Cloutier et al. (2008) and Vartanian et al. (2013) found significant modulation of the BOLD signal in prefrontal cortices during explicit decisions about facial attractiveness, with activation in frontal poles (mainly corresponding to BA10) increasing parametrically with increase in attractiveness judgments. The authors argued that frontal activity during attractiveness judgments may be related to mentalizing processes as the act of making self-referential evaluative judgments (see also Martín-Loeches et al., 2014). Finally, electrophysiological studies confirm the involvement of the frontal areas in explicit evaluation of facial attractiveness already at early stages of processing (e.g., 150–200 ms; see Marzi and Viggiano, 2010).

In this study we aimed to determine whether the prefrontal cortices play a causal role in attractiveness judgments of faces by using transcranial direct current stimulation (tDCS). tDCS is a method used to modulate cortical excitability of a targeted region in a safe, non-invasive and reversible way. As other brain stimulation techniques, tDCS is able to induce observable behavioural changes, thus extending neuroimaging and electrophysiological evidence by shedding light on the *causal* role of a specific brain region in mediating a certain function/task (e.g., Miniussi et al., 2013). In our study, participants had to indicate how attractive they found a series of faces, both before and after receiving (real or sham) anodal tDCS over the dorsolateral prefrontal cortex (DLPFC). We used anodal tDCS because the resulting increase in cortical excitability of non-motor cortical areas has been largely confirmed, whereas the effects of cathodal tDCS are more debated (for a review, see Jacobson et al., 2012). To ascertain the specificity of tDCS effects on appraisals of attractiveness, in a second, control, experiment we required participants to estimate face age (see Winston et al., 2007, for a similar control task). If tDCS over the DLPFC cortex affects both attractiveness and age judgments, this would indicate that the stimulation effects are not task-specific but generalize to explicit decisions about different facial attributes. Finally, given that prior brain stimulation studies reported gender differences in hemispheric asymmetry of brain activity associated to the aesthetic evaluation of bodies (Cazzato et al., 2014), we recruited an equal number of male and female participants to be able to investigate possible gender-related differences in lateralization during subjective evaluation of facial attractiveness.

2. Experiment 1

2.1. Method

2.1.1 Participants

Twenty participants (10 F, mean age=22.9, SD=1.9) volunteered to participate in this study. They were all right handed (Oldfield, 1971), all had normal or corrected to normal vision and reported to have normal colour vision. Prior to the experiment, each participant filled out a questionnaire with regard to the inclusion and exclusion criteria concerning the application of tDCS. Written informed consent was obtained from all participants. The experiment was approved by the local ethical committee and subjects were treated in accordance with the Declaration of Helsinki.

2.1.2 Stimuli

Stimuli consisted of 280 photographs of unfamiliar faces of young (age range: 19–30 yr) Caucasian individuals. Half of them were males and half females. Pictures were taken from publicly available face databases (e.g., Minear and Park, 2004), from the web or were taken by the authors themselves. Overall, faces were of average attractiveness, with the exception of some faces of fashion models (approximately 5% of the stimuli) that were highly attractive. We chose not to only focus on extremely attractive or unattractive faces for ecological validity (see also Vartanian et al., 2013). All faces were presented in a frontal view on a light grey background, had a neutral expression and were free of jewellery, glasses, evident make up, tattoos, or overly conspicuous hairstyles. The faces were divided into two sets of 140 photographs, each containing an equal number of male and female faces. The two sets were equivalent in terms of attractiveness, as assessed by a rating pilot study in which 12 raters (6 F, mean age=22.3, SD=1.2), none of which took part in the tDCS experiment, were asked to rate a larger set of faces from which the two final sets were then obtained.

2.1.3 Procedure

Participants were seated in front of a 15.5″ PC screen (1280*800 pixels) at an approximate distance of 57 cm, in a normally lit and silent room, and asked to perform a computerized rating task. Before starting the experiment, participants were informed that they would be viewing the same set of faces twice, once before and once after stimulation (see below), and that their task was to express how attractive they found each specific face. Fig. 1 shows the timeline of an experimental trial. Each trial started with the presentation of one of the faces that appeared on a grey background and subtended a visual angle of $7 \times 7°$. A horizontal rating bar appeared below each picture (see Fig. 1).

Participants were informed that the bar was meant to express a 0–100% scale: the left end of the bar corresponded to a zero level of attractiveness (i.e., this face *to me* is completely unattractive) whereas the right end of the bar corresponded to the maximum level of attractiveness (i.e., this face *to me* is completely attractive). Participants were instructed to express their judgment by clicking with the mouse using their right hand. The mouse cursor was a fully vertical arrow that appeared under either the left or the right extreme of the line and moved only horizontally. The initial position (left or right) of the cursor was randomly assigned for each trial. The image remained visible until participants expressed their judgment. After responding, the screen was cleared-out for 300 ms, after which a new image was presented. There was no time limit, but participants were encouraged not to delay their responses. Images were presented in random order. Before starting each task, participants were informed that the set of faces they had to evaluate mainly included faces of average attractiveness,

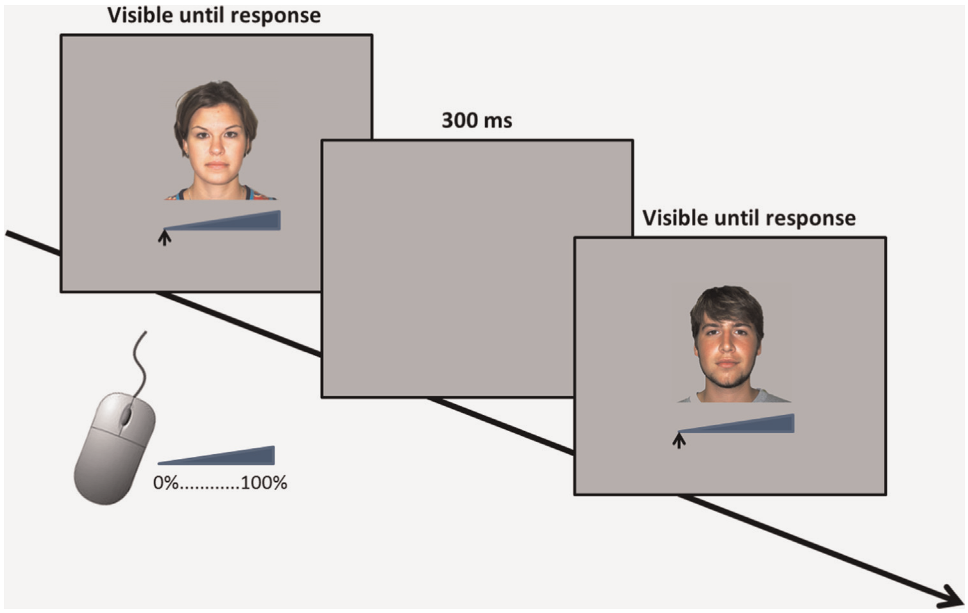

Fig. 1. Example of an experimental trial. In each trial a face was presented in the middle of the screen and participants had to indicate, by moving the mouse cursor along a rating bar, how attractive it was (Experiments 1 and 2), or its estimated age (Experiment 3). The left end of the rating bar corresponded to 0% score (i.e., "This face to me is completely unattractive" in Experiments 1 and 2 and "0 yr" in Experiment 3). The right end of the rating bar corresponded to 100% score ("This face to me is completely attractive" and "100 yr"). Within the experiment, the mouse arrow appeared randomly an equal number of times below the left or the right end of the rating bar. The two faces shown in the Figure are from the Minear and Park (2004) database.

but that also some high attractive faces (models) could be presented. Thereafter, two practise trials were performed (showing faces not included in the main experiment) to familiarize participants with the rating procedure. The whole experiment lasted approximately 45 min. For each participant, the set of presented faces was different in the two stimulation sessions (real and sham, see below). The order of presentation of the two sets was counterbalanced across participants. The software E-prime 2.0 (Psychology Software Tools, Inc., Pittsburgh, PA, USA) was used for stimuli presentation and data recording.

2.1.4 tDCS

tDCS was delivered by a battery driven, constant current stimulator (Eldith, Neuroconn, Ilmenau, Germany) through a pair of saline-soaked sponge electrodes (7×5 cm: 35 cm^2) kept firm by elastic bands. The excitability-enhancing anodal electrode was placed over the left DLPFC localized as the middle point between F3 and F5 in the 10-20 EEG system (roughly corresponding to the juncture of BAs 9 and 46, see Rusjan et al., 2010), while the cathodal electrode was placed over the controlateral supraorbitary region. This electrode arrangement is thought to induce unilateral modulation of one DLPFC and has been shown effective in various studies (Fecteau et al., 2007; Fregni et al., 2005; Kincses et al., 2004). Each participant underwent two stimulation sessions: a real one and a sham one. In each session, participants performed the task twice: once before stimulation, and once after stimulation. Sessions were separated by an average of 3.5 days (Range: 2–5 days). The order of stimulation sessions was counterbalanced across participants, such that half-started with the sham session and the other half-with the real session. In the real tDCS session, stimulation intensity was set at 2 mA and the duration of stimulation was 20 min. For the sham stimulation, the electrodes were placed at the same positions as for active stimulation, but the stimulator was turned on only for 30 s. Thus, participants felt the initial itching sensation associated with tDCS, but received no active current for the rest of the stimulation period. This procedure prevents any effective modulation of cortical excitability by sham tDCS, allowing for a successful blinding of participants for the real vs. sham stimulation condition (Russo et al., 2013). Participants watched a cartoon movie while stimulation was administered to ensure that all participants were exposed to the same visual experience during stimulation reducing inter-subject variability (e.g., Cattaneo et al., 2014a; Renzi et al., 2013, for a similar procedure). The cartoon movie finished shortly before the end of the tDCS and the participants were told that in few seconds they would have to perform the task again. The study was a single-blind experiment: participants were not aware of the type of stimulation they received, whereas the experimenter was fully informed.

2.2. Results

The position of the mouse cursor along the bar was automatically converted by the software to percentage rating scores, where a 0% score corresponded to the mouse cursor positioned at the left end of the rating bar and a 100% score corresponded to the mouse cursor positioned at the right end of the rating bar. Trials in which participants' response latencies (RT) were 3SD over their own average response time were excluded from the analyses (1.48% of trials were excluded following this criterion). Mean attractiveness scores were 34.3% (SD=14.7) and 33.4% (SD=14.8) for pre- and post-sham tDCS, and 34.4% (SD=12.1) and 33.7% (SD=14.2) for pre- and post-real stimulation. A repeated-measures ANOVA was performed on the difference in rating scores between post- and pre-stimulation with tDCS (real and sham) and sex of the face as within-subjects variables and participants' sex as between-subjects variable (see Fig. 2). The effect of tDCS was not significant, $F(1,18) < 1$, $p=.81$, $\eta_p^2=.00$, indicating that real and sham tDCS had similar effects. The difference between pre- and post-tDCS attractiveness scores was comparable for male and female faces, $F(1,18)=2.25$, $p=.15$, $\eta_p^2=.11$, and was not affected by participants' sex, $F(1,18) < 1$, $p=.46$, $\eta_p^2=.03$. None of the interactions reached significance (all $ps > .18$). Although attractiveness scores were, overall, slightly lower in the post-compared to the pre-sessions (see Fig. 2), a one-sample t-test against zero showed that this difference (collapsed across real and sham tDCS) was not significant, $t(19) < 1$, $p=.37$.

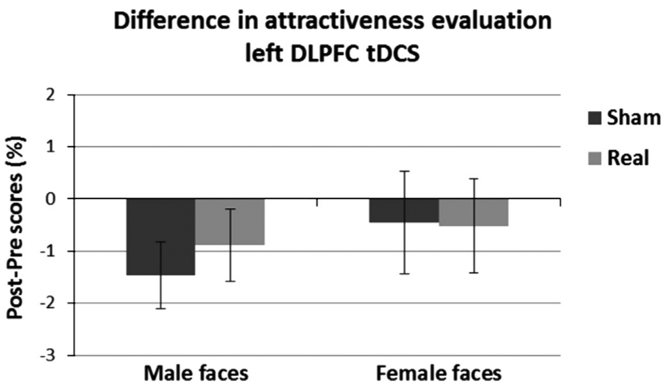

Fig. 2. Difference (=post-pre) in attractiveness scores between post- and pre-stimulation of the left DLPFC (Experiment 1). Real and sham stimulation on the left DLPFC had similar effect on performance. Error bars represent ± 1 SEM.

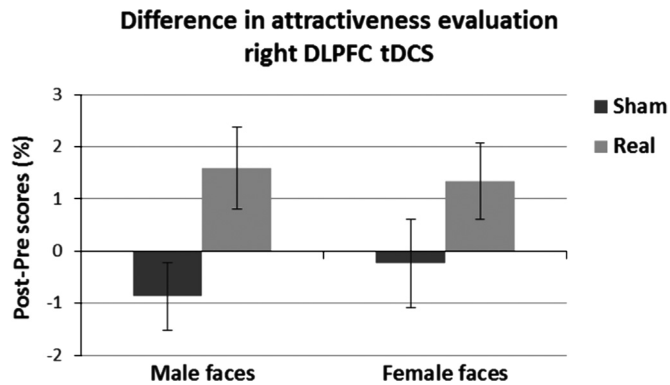

Fig. 3. Difference in attractiveness scores between post- and pre-stimulation of the right DLPFC (Experiment 2). Real tDCS over the right DLPFC induced an increase in perceived face attractiveness compared to the sham stimulation. Error bars represent ± 1 SEM.

Mean response latencies (RT) were 2636 ms (SD=1263) and 2293 ms (SD=1195) for pre- and post-sham tDCS, and 2736 ms (SD=1231) and 2403 ms (SD=1228) for pre- and post-real tDCS. The ANOVA on the difference in RT between post- and pre-tDCS revealed no significant effect of tDCS, $F(1,18) < 1$, $p = .95$. Neither the main effect of sex of the face ($p = .11$), nor the main effect of participants' sex ($p = .52$) were significant. None of the interactions approached significance (all $ps > .07$). A one-sample t-test against zero revealed that the fastening (mean=338 ms) in RT between pre- and post-tDCS (collapsed across real and sham tDCS) was significant, $t(19) = 3.19$, $p = .005$, likely reflecting learning or familiarity effects.

3. Experiment 2

In Experiment 1, no effects of tDCS over the left DLPFC were observed on facial attractiveness judgments. In Experiment 2, the same paradigm was used, except that stimulation was applied over the right DLPFC.

3.1. Method

3.1.1 Participants

Twenty right-handed participants (10 F, mean age= 24.0 yr, SD=2.6), all with normal or corrected-to-normal vision, all meeting criteria for tDCS stimulation (see Experiment 1), took part in Experiment 2. None of the participants of Experiment 2 had taken part in Experiment 1. Written informed consent was obtained from all participants.

3.1.2 Stimuli and procedure

Stimuli and procedure were the same as for Experiment 1. tDCS was applied as in Experiment 1, but this time the anode was applied over the right DLPFC localized as the middle point between F4 and F6 in the 10-20 EEG system, while the cathodal electrode was placed over the left supraorbitary region.

3.2 Results

Data were analyzed as in Experiment 1. In 1.64% of the trials participants' RT were 3SD over their own average response time; these trials were excluded from the analyses. Mean appreciation scores were 36.7% (SD=9.9) and 36.2% (SD=9.3) for pre- and post-sham tDCS, and 36.1% (SD=8.6) and 37.6% (SD=9.7) for pre- and post-real stimulation. A repeated-measures ANOVA on the difference in rating scores between post- and pre-stimulation with tDCS (real and sham) and sex of the face as within-subjects variables and participants' sex as between-subjects variable revealed a significant effect of tDCS, $F(1,18) = 5.04$, $p = .038$, $\eta_p^2 = .22$, due to real tDCS significantly increasing attractiveness ratings compared to sham tDCS (see Fig. 3). The difference in rating between pre- and post-session was not affected by either participants' sex, $F(1,18) < 1$, $p = .39$, $\eta_p^2 = .04$, or sex of the faces, $F(1,18) < 1$, $p = .71$, $\eta_p^2 = .01$. None of the interactions reached significance (all $ps > .07$). One-sample t-tests against zero (i.e., comparable liking prior and post-tDCS) revealed that aesthetic evaluation of faces did not differ significantly between post- and pre-stimulation, $t(19) < 1$, $p = .38$. In turn, liking of faces increased following real tDCS, with difference between post- and pre-liking scores approaching significance, $t(19) = 2.03$, $p = .057$.

In order to assess whether the effects of tDCS depended on the attractiveness rating at baseline, we carried out a correlational analysis (Pearson, two-tailed) to verify whether the increment in attractiveness rating induced by real tDCS depended on initial (pre-tDCS) liking of that specific face. The analysis revealed that the effects of tDCS were not significantly affected by the initial level of liking of the faces, $r(278) = -.109$, $p = .069$.

Mean RT were 2478 ms (SD=1089) and 1950 ms (SD=648) for pre- and post-sham tDCS, and 2426 ms (SD=969) and 2025 ms (SD=707) for pre- and post-real tDCS. The ANOVA on the difference in mean RT between post- and pre-tDCS revealed no significant effect of tDCS, $F(1,18) < 1$, $p = .50$, and no significant effects of either sex of the face ($p = .09$) or sex of the viewer ($p = .88$). None of the interactions approached significance (all $ps > .52$). A one-sample t-test against zero revealed that the fastening (=465 ms) in RT between pre- and post-tDCS (collapsed across stimulation type) was significant, $t(19) = 5.06$, $p < .001$. Again, this is probably related to learning/familiarity effects.

4. Experiment 3

In order to verify whether the effects of tDCS on the right DLPFC reported in Experiment 2 are specific for face-attractiveness judgments, or also apply to judgments on other aspects of faces, we carried out a control experiment in which participants were required to judge the age of faces while tDCS was applied as in Experiment 2.

4.1. Method

4.1.1 Participants

Eighteen right-handed participants (9 M, mean age= 24.9 yr, SD=3.6), all with normal or corrected-to-normal vision, all meeting criteria for tDCS stimulation, took part in Experiment 3. None of the participants of Experiment 3 had taken part in the prior two Experiments. Written informed consent was obtained from all participants.

4.1.2 Stimuli and procedure

Stimuli consisted of pictures of 272 Caucasian faces, half-male and half-female. Faces were all taken from the database by Minear and Park (2004), which specifies the age for each face. The age of the people whose faces are included in the database ranged from 18 to 91 yr (specifically, we took 88 faces in the 18–26 yr range bin; 42 faces in the 27–49 yr bin; 55 faces in the 50–69 yr bin; and 87 faces in the 70–91 yr bin; age range bins as provided by Minear and Park, 2004). In accordance with the aims of the tDCS design, two sets of 136 faces, balanced in terms of faces age and sex, were created. The procedure was similar to that used in the first two Experiments. In this case, however, participants were required to indicate, using the evaluation bar, the estimated age of each face, and were instructed that the left end of the bar meant 0 yr, and the right end of the bar meant 100 yr. Six practice trials (with faces different from those used in the main experiment) were presented before the actual experiment to familiarize participants with the task. tDCS was delivered over the right DLPFC as described in Experiment 2.

4.2 Results

Analyses were performed on participants' age estimated scores (scores computed by the software as in Experiments 1 and 2). Trials in which participants' RT were 3SD over their own average response time were excluded from the analyses (1.63% of the trials were excluded).

Data were analyzed using a repeated-measures ANOVA on the difference in mean estimated age scores between post- and pre-sessions, with tDCS (real and sham) and sex of the face as within-subjects variables, and participants' sex as between subjects variable. The results revealed no significant main effect of either tDCS, $F(1,16) < 1$, $p=.50$, $\eta_p^2=.03$, or sex of the face, $F(1,16)=2.65$, $p=.12$, $\eta_p^2=.14$, or participants' sex, $F(1,16) < 1$, $p=.36$, $\eta_p^2=05$. None of the interactions reached significance (all $ps > .12$) (see Fig. 4). One-sample *t*-tests against zero (i.e., comparable age estimation prior and post-tDCS) revealed that participants judged the faces as significantly younger in the post-compared to the pre-session (irrespective of stimulation being real or sham), $t(17)=2.22$, $p=.040$. This difference likely reflected learning effects: indeed, participants tended to overestimate age of the faces on average of 6.77 yr (SD=3.61) compared to the true age provided in the database, responding slightly closer to the real age the second time they saw the face (mean error=6.28 yr, SD=3.73).

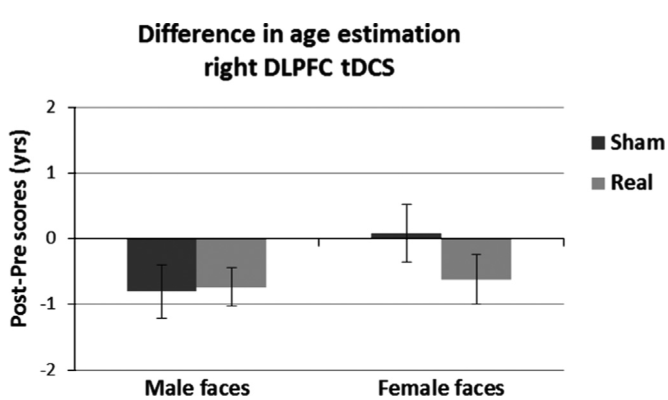

Fig. 4. Difference in age estimation (years) in the age evaluation task of Experiment 3 between post- and pre- stimulation. tDCS over the right DLPFC had no effect on participants' judgments. Error bars represent ± 1 SEM.

Mean response times were 2848 ms (SD=1044) and 2453 ms (SD=905) for pre- and post-sham tDCS, and 2855 ms (SD=1337) and 2522 ms (SD=879) for pre- and post-real tDCS. The ANOVA on the difference in mean RT between post- and pre-tDCS revealed no significant effect of tDCS, $F(1,16) < 1$, $p=.70$. Sex of the faces ($p=.14$) and sex of the observer ($p=.96$) were not significant. None of the interactions reached significance (all $ps > .14$). The reduction in RT (=364 ms) between pre- and post-tDCS (irrespective of stimulation type) was significant, $t(17)=4.03$, $p=.001$, again likely reflecting learning effects.

5. Discussion

We found that increasing excitability in the right DLPFC via anodal tDCS led to an increase in perceived attractiveness of faces (Experiment 2). In turn, tDCS over the left DLPFC did not modulate facial attractiveness appraisals (Experiment 1). The effect of tDCS over the right DLPFC was not modulated by either participant's sex or the sex of the face displayed, nor did it depend on the faces' initial attractiveness level. In a control experiment (Experiment 3), anodal tDCS over the right DLPFC did not affect the estimation of faces' age, suggesting that the effects of anodal tDCS on appraisals of facial attractiveness did not depend on stimulation affecting decisions in general about other facial attributes. Also, it is unlikely that response modality affected the pattern of results we reported. More specifically, if the effects of tDCS on the appraisal of facial attractiveness depended on tDCS shifting attention (and response) to the rightward end of the bar, a similar pattern should have also emerged during the age task. Overall, thus, our data point to a *causal* role of the (right) DLPFC in explicit facial attractiveness judgments, extending prior neuroimaging evidence reporting activation in dorsolateral prefrontal regions during facial attractiveness appraisals (e.g., Chatterjee et al., 2009; Cloutier et al., 2008; Martín-Loeches et al., 2014; for reviews see Bzdok et al., 2011 and Mende-Siedlecki et al., 2013).

Although there was some variation in the extent to which faces were liked when evaluated for the first vs. the second time, the differences in evaluation were not significant between pre- and post-sham right prefrontal stimulation, nor between pre- and post (sham or real) left tDCS. In turn, the increment in attractiveness ratings following real tDCS over the right DLPFC approached significance ($p=.057$). This finding suggests that the main difference between real and sham tDCS observed when targeting the right DLPFC was not merely due to summation of opposite tendencies: real tDCS did indeed increase attractiveness ratings compared to first (pre-tDCS) evaluation. Still, this increase may have been partially attenuated by a (non-significant) tendency to award slightly lower ratings upon second presentation, as consistently observed in sham conditions across the first two experiments. But why did increasing excitability of the DLPFC lead participants to appraise the faces as more attractive? And why was this effect lateralized to the right hemisphere?

The effects we reported may be related to the role of the DLPFC in value decision making and to the connections between DLPFC and other brain regions that are more directly involved in reward/value computation. Attractiveness is a source of reward for humans, and as such, it is a “value” to be pursued (e.g., Wilson and Daly, 2004). Decisions about facial attractiveness rely on activity throughout the reward system, including the orbitofrontal (OFC) cortex (e.g., Aharon et al., 2001; Cloutier et al., 2008; Kampe et al., 2001; Kranz and Ishai, 2006; Martín-Loeches et al., 2014; O'Doherty et al., 2003; Winston et al., 2007), and the functional connectivity between the DLPFC and the OFC is well documented (e.g., Hare et al., 2009; Weber et al., 2014). More specifically, for value computation, it has been suggested that the DLPFC may send signals to the OFC, where they are integrated together with inputs from other areas, to compute goal value (Hare et al., 2009). In line with this, Camus et al. (2009) reported that inhibiting activity in the right DLPFC via transcranial magnetic stimulation (TMS) produced a significant decrease in the values assigned to food (reward) stimuli, and suggested that this effect was due to diminished inputs from the DLPFC to the OFC. Although value computation mechanisms are certainly different for food and faces (they are rewarding in different ways), our findings may be interpreted in light of the study performed by Camus et al. (2009), which suggested that increasing activity in the right DLPFC produces increased value (attractiveness) attribution to the stimuli. This interpretation would account also for the lack of stimulation effects on the age judgment task. Age estimations require a visual analysis, but there is no “value” that enters the decision making process. Accordingly, prior findings showed that facial age evaluation involved more posterior than anterior cortical sites (Homola et al., 2012).

In our experiment, tDCS over the right DLPFC affected male and female participants in a similar manner. In a recent TMS study, Cazzato et al. (2014) reported a right-hemisphere lateralization in female viewers, though not in males, of activity in the extrastriate body area during aesthetic appreciation of human bodies. It is possible that gender related differences in hemispheric lateralization during aesthetic evaluation are limited to more posterior cortical regions, and that they depend on the specific class stimulus being evaluated (see also Cela-Conde et al., 2009). In line with our findings, prior neuroimaging studies have not reported differences in hemispheric asymmetry between male and female observers during the implicit or explicit evaluation of facial attractiveness (e.g**.**, Chatterjee et al., 2009**;** Vartanian et al., 2013)**.**

The effect of tDCS on the right DLPFC was not modulated by the sex of the faces. Senior’s (2003) facial attractiveness model suggests that once attractiveness is appraised, it may be computed both as reward and as aesthetic value. This implies that the rewarding, adaptive value of an attractive face can be dissociated from its “purely” aesthetic value (see also Aharon et al., 2001). This dissociation is reflected at the neural level by a different pattern of activation and deactivation in certain regions of the reward circuit (such as the sublenticular nucleus of the amygdala and the nucleus accumbens, see Aharon et al., 2001 and Senior 2003). Also, several regions responding to facial attractiveness, such as the OFC, have been found to respond similarly to high attractive faces regardless of the sex of the viewers and the sex of the faces (see O’Doherty et al., 2003). Given the lack of sex-related modulation on the effects of tDCS in our study, we conjecture that tDCS biased the underlying system involved in aesthetic evaluation further toward the “liking” rather than the “wanting”/reward-expecting mode of processing (see Berridge, 1996 and Aharon et al., 2001). Similarly, the DLPFC activation typically observed in neuroimaging studies during aesthetic appreciation of artworks has been interpreted as reflecting the switching from a “pragmatic orientation” to an “aesthetic orientation” (Cupchik et al., 2009), a switch that can be enhanced by tDCS (see Cattaneo et al., 2014a) or suppressed by TMS (Cattaneo et al., 2014b). Winston et al.'s (2007) fMRI study is relevant to this point. They observed an unexpected pattern for which actually attending to facial attractiveness appeared to diminish activity in at least some reward-related areas and conjectured that the reward value of a visual stimulus could be diminished when trying to evaluate it.

Some previous neuroimaging studies found a prefrontal involvement in face attractiveness judgments preferentially lateralized to the left hemisphere (e.g., Nakamura et al., 1998; Vartanian et al., 2013), and brain stimulation studies reported that modulating activity in the left prefrontal cortex affected aesthetic judgments of paintings (Cattaneo et al., 2014a, 2014b). In contrast, in our study tDCS over the left prefrontal cortex did not modulate participants' evaluation of facial attractiveness. Given that the face network is mainly right-lateralized (Haxby et al., 2000) it may be the case that the right prefrontal cortex has a stronger role in aesthetic computation when faces are the objects of the evaluation than the left prefrontal cortex. An alternative explanation for the lateralized effects we reported is related to the mechanisms that mediate face processing *per se*. Previous neuroimaging and brain stimulation studies suggest that the right DLPFC is more involved in processing configural/holistic aspect of faces, whereas the left prefrontal cortex is more involved in processing single facial features (Maurer et al., 2007; Renzi et al., 2013). Although evaluation of single facial features are certainly involved in perceiving a face as attractive, models of aesthetic appreciation of faces suggest that facial attractiveness is mainly based on a configural evaluation (see Abbas and Duchaine, 2008; Penton-Voak et al., 2001). Therefore, it is possible that increasing activity in the right prefrontal cortex biased the system toward a more holistic mode of processing, and that this led to an increase in the appraisal of facial attractiveness.

In interpreting our results, some caveats need to be acknowledged. Most of the faces (more than 70%) received overall low-medium attractiveness scores (below the value of 50 on the evaluation bar). The faces we used were from averagely attractive individuals. However, before starting the test, participants were informed that they would also have to rate faces of models (hence, highly attractive). It is likely that this *a-priori* knowledge biased scores to the “low-end” because participants adjusted their evaluation criterion considering the very attractive faces. Moreover, all faces appeared in a close frontal view, with no make-up (for female faces) and – importantly – no smile. All these factors may have reduced the perceived attractiveness of the faces (with smile, for instance, usually increasing the reward value of a face, see Jones et al., 2006). We cannot rule out the possibility that using a stimuli set of only highly attractive faces may lead to an engagement of the reward system to a greater extent (see Aharon et al., 2001) thereby also altering the effects of tDCS. Future studies are required to shed light on this issue. Still, our aim was to examine the brain mechanisms mediating aesthetic appreciation under more ecological conditions, where we are usually confronted with averagely attractive faces.

Moreover, although in our study we only focused on facial attractiveness we cannot exclude that the tDCS effects we observed also extend to aesthetic evaluation of persons in general. Indeed, a prior TMS study (Calvo-Merino et al., 2010) found that stimulation of the inferior frontal gyrus affected aesthetic evaluation of bodies. Finally, in considering our results, it is important to mention that imaging evidence suggests that DLPFC tDCS affects other cortical and subcortical sites beyond the targeted region, modulating resting-state functional connectivity in distinct functional brain networks (e.g., Keeser et al., 2011; Romero Lauro et al., 2014; Stagg et al., 2013). In particular, using a montage and stimulation parameters similar to those used here, Keeser et al. (2011) found that anodal tDCS over the left DLPFC induced significant changes of regional brain connectivity in both left and right frontal-parietal networks. Still, using functional near-infra-red spectroscopy (fNIRS), Merzagora et al. (2010) found that anodal stimulation of the DLPFC produced a greater increase in oxyhemoglobin concentration in the areas under the anode. Moreover, prior studies found that tDCS effects on behaviour were specific to the site of stimulation, and were different from those obtained by stimulating a nearby region in the same hemisphere (e.g., Fregni et al., 2005; Javadi and Walsh, 2012; Pisoni et al., 2012). Also, different effects of anodal tDCS on left and right DLPFC have been reported before (e.g., Fecteau et al., 2007; Giglia et al., 2014). In light of this, we interpret our findings as to be mainly dependent on modulation of activity in the right DLPFC, although we cannot rule out the possibility that tDCS affected larger cortical and subcortical networks, also in the contralateral hemisphere.

In conclusion, our results provide evidence that perceived facial attractiveness can be enhanced by applying transcranical direct current stimulation over the right dorsolateral prefrontal cortex, extending previous neuroimaging and electrophysiological evidence, and shedding light on the complex system that mediates the appraisal of facial attractiveness.

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