# Testing the *immediate* effects of transcranial Direct Current Stimulation (tDCS) on face recognition skills.

# Ciro Civile (c.civile@exeter.ac.uk)

School of Psychology, College of Life and Environmental Sciences, University of Exeter, UK.

## R. McLaren (r.p.mclaren@exeter.ac.uk)

School of Psychology, College of Life and Environmental Sciences, University of Exeter, UK

# Emika Waguri (ew518@exeter.ac.uk)

School of Psychology, College of Life and Environmental Sciences, University of Exeter, UK.

# I.P.L. McLaren (i.p.l.mclaren@exeter.ac.uk)

School of Psychology, College of Life and Environmental Sciences, University of Exeter, UK.

#### **Abstract**

In the present study, we tested the effects of anodal tDCS delivered over the Fp3 (for 10mins at 1.5mA) on the face inversion effect (better recognition for upright vs inverted faces) while participants performed an old/new recognition task. We recruited three groups of participants (n=72) and randomly assigned them to experimental conditions. In the anodal Study Phase condition participants received the tDCS stimulation during the learning phase only. In the anodal Recognition Phase condition, participants received the anodal stimulation during the recognition task only. In the control group participants received sham stimulation (during the study or recognition phase). Consistent with previous research, the results showed that anodal stimulation reduced the inversion effect by impairing recognition of upright faces. Critically, in both anodal conditions the inversion effect was significantly reduced compared to sham, and no difference was found between the two anodal conditions. Upright faces in each anodal condition were recognized significantly worse than sham. This suggests that the tDCS-induced effects on face recognition are immediate and affect both learning and performance. We interpret the results based on the account of perceptual learning and previous work on tDCS and the inversion effect.

Keywords: Face Inversion effect; tDCS; perceptual learning

# Introduction

Faces as a set of "stimuli" have been employed in several different ways to investigate the specific processes underpinning our remarkable ability to recognize faces. One of the most widely used experimental manipulations in the literature is to simply turn a set of faces upside-down and ask participants to try to recognize them. This led to the discovery of the robust cognitive phenomenon known as the face inversion effect (Yin, 1969; Civile, McLaren, McLaren, 2014; Civile, McLaren, McLaren, 2016). This refers to the reduced recognition performance for inverted face images compared to faces presented in their usual upright orientation. The first key finding was that this effect was larger for faces than for several other categories of stimuli (e.g. houses or planes) suggesting that it could be used as an index of the "specific" nature of our face recognition skills (Scapinello & Yarmey, 1970; Valentine & Bruce, 1986; Haxby, Hoffman & Gobbini, 2000; Yovel & Kanwisher, 2005). Several authors have

challenged this interpretation by showing that a robust inversion effect similar to that obtained for faces can be generated with other sets of stimuli. An important study conducted by Diamond and Carey (1986) was the first to provide some clear evidence in support of this. The authors were able to demonstrate as large an inversion effect for dog images as that for human faces when participants were experts (i.e. dog breeders) at judging (at dog shows) the type of dog breed presented. These participants had a great deal of experience with this type of dog, and hence had seen many more of them than the average person. Thus, the authors suggested "expertise" as one of the determining factors for our ability to recognize faces, we are good at this because we have so much experience with this type of stimulus. Importantly, in 1997 Gauthier and Tarr introduced a new line of research based on training participants with a specially designed class of mono-orientated stimuli named Greebles. Participants, who had been exposed to upright Greebles detected changes faster for upright than for inverted stimuli; novices did not differ in their performance across orientations. In a similar vein, Gauthier et al (1998) engaged Greeble experts and novices in a recognition task. At first both participant groups showed only a small benefit (in RT responses) in responding to upright Greebles vs rotated ones (60, 120 and 180 degrees). Following training, recognition performance became faster with practice for both groups, however, experts (those with a lot of experience of Greebles) now showed a greater advantage for upright Greebles which then led to a larger inversion effect (compared to novices) when the stimuli were presented inverted. Taken all together, Diamond and Carey (1986), Gauthier and Tarr (1997), Gauthier et al (1998)'s work provides support for the expertise account of face recognition (see also Tanaka and Farah, 1991 for an example of an inversion effect with configurations of dot patterns). In parallel with Gauthier's work with Greebles, in 1997, McLaren provided the first evidence of a large inversion effect for non mono-orientated prototype-defined categories of artificial stimuli (checkerboards) that was predicted by a model of perceptual learning, the MKM model (McLaren, Kaye & Mackintosh, 1989; McLaren & Mackintosh, 2000). In recent years, Civile, Zhao, et al (2014) extended McLaren

(1997)'s findings by adopting an old/new recognition task of the same type as that often used in the literature to obtain the inversion effect (Yin, 1969; Diamond & Carey, 1986; Robbins & McKone, 2007; Civile, McLaren, & McLaren, 2011). Participants were first given a categorization task (preexposure phase) that required them to learn to distinguish between checkerboard exemplars derived from two different prototype-define categories. Following this, there was a *study* phase where a set of checkerboards was presented one at a time and participants were asked to memorize them. Some of the checkerboards presented were new exemplars drawn from one of the two familiar categories previously encountered during the categorization task. Half of these "familiar" checkerboards were presented upright (same orientation as that familiarized during the categorization task) and the other half were presented inverted. A baseline for assessing performance was provided by checkerboards drawn from a novel prototype-defined category (not seen in the categorization task) that were also presented in this study phase. As for the checkerboard exemplars taken from a familiar category, some of the exemplars from the novel category were presented upright and some inverted. In the final phase, the old/new recognition task, participants were asked to recognize checkerboards that included the same exemplars previously seen in the study phase (i.e "old"), intermixed with some "new" checkerboards selected according to the same four stimulus conditions (i.e. familiar upright/inverted, novel upright/inverted). A large inversion effect was found for exemplars drawn from the familiar category whereas no inversion effect was found for exemplars drawn from the novel category (Civile, Zhao et al., 2014). The results from McLaren (1997), and Civile et al (2014) bring additional support to the expertise account of face recognition, and they have also served as the basis for further investigations of face and object recognition using transcranial Direct Current Stimulation (tDCS).

This new line of research has shown how tDCS can be used to investigate face recognition skills. The typical tDCS montage consists of placing two electrodes (i.e. the target channel and the reference/return channel) on the surface of the scalp and delivering a continuous non-invasive low electrocurrent stimulation through them. In most studies the amplitude of the stimulation ranges between 1-2mA (Nitsche et al., 2008). When anodal tDCS stimulation is delivered, the electro-current is believed to induce a depolarization of the resting membrane potential which in turn modulates cortical excitability. The sham (control) stimulation lasts for a brief period of time, usually 30 seconds, and it remains off for the rest of the stimulation time. The sham procedure is supposed to give participants the feeling of being stimulated, although they are not receiving prolonged continuous stimulation (Radman et al., 2009). Ambrus et al (2011) showed that anodal tDCS delivered over the left dorsolateral prefrontal cortex (DLPFC) at Fp3 site can eliminate the prototype distortion effect (higher performance at categorizing category prototypes compared to category exemplars, neither of which had been previously seen) by affecting individuals' ability to identify prototype and low distortion pattern exemplars as

category members compared to sham. The authors targeted this specific region based on a previous fMRI study showing increased brain activation during a category learning task involving two sets of prototype-defined categories of colored checkerboards. The left DLPFC was found to be highly activated in participants who showed a high level of categorization performance (Seger et al., 2000).

In recent years, researchers have directly investigated the influence of tDCS on the face inversion effect. Civile, Verbruggen, et al (2016) extended the tDCS procedure used by Ambrus et al (2011) Kincses et al (2013) and McLaren et al (2016) to modulate categorization skills for prototypedefined pattern exemplars, to the same inversion effect paradigm for checkerboards developed by Civile, Zhao et al (2014). They demonstrated that Anodal tDCS delivered over the DLPFC at Fp3 site for 10 mins at an intensity of 1.5mA eliminated the inversion effect usually found for familiar checkerboards by reducing performance for upright checkerboards compared to sham. Perhaps the most important finding in this line of research is that first presented by Civile, McLaren, and McLaren (2018), then replicated in Civile, Obhi, McLaren (2019) and extended by Civile, Cooke et al (2020). Using a series of double-blind and between-subjects experiments the authors were able to establish that the same tDCS procedure adopted in Civile, Verbruggen et al (2016) can significantly reduce the robust inversion effect traditionally found for face stimuli. Once again the anodal tDCS stimulation disrupted performance for the upright stimuli (in this case faces) compared to that for sham (Civile et al., 2018; Civile et al., 2019; Civile, Cooke et al., 2020. Experiment 3a). Importantly, with an active control study (double-blind and between-subjects) Civile et al (2018) also demonstrated that applying the same tDCS anodal stimulation to a different targeted area did not result in any modulation of the face inversion effect compared to the sham group.

Furthermore, in recently published work, Civile, Waguri et al (2020) investigated the electrophysiological correlates of the tDCS-induced effects on the face inversion effect. The authors combined DCS and EGG simultaneously while participants performed the same old/new recognition task involving upright and inverted faces used by Civile et al (2018). The results from two studies have shown that the anodal tDCS procedure previously adopted by Civile, Verbruggen et al (2016), Civile et al (2018), Civile et al (2019), and Civile, Cooke et al (2020) can influence the face inversion effect on the N170 ERP component recorded at the P08 channel. Specifically, a dissociation was found where for the N170 latencies the tDCS procedure reduced the usual face inversion effect (delayed N170 in response to inverted vs. upright faces) compared to sham. Contrarily, the same tDCS procedure on the same participants increased the inversion effect seen in the N170 amplitudes (larger N170 peak for inverted vs upright faces) compared to sham (Civile, Waguri et al., 2020).

Overall, the research reported in Civile, Verbruggen et al (2016), Civile et al (2018), Civile et al (2019), and Civile, Cooke et al (2020) is important because it strengthens the analogy between the inversion effect for checkerboards and

the traditional inversion effect for faces, by demonstrating that they both share at least some aspects of the same causal mechanism. This also strengthens the case for there being a component of the face inversion effect based on perceptual learning. Furthermore, recent work by Civile, Waguri et al (2020) presents the first evidence in the literature for the specific tDCS procedure to be able to influence the face inversion effect behaviorally and on the ERPs N170 peak component.

In the study reported here, we extended the research on tDCS and the face inversion effect by investigating directly whether the tDCS-induced behavioral effects are immediate or need time to build up. Hence, we adopted the exact same tDCS procedure, and old/new recognition behavioural paradigm and same stimuli, as that in Civile et al (2018), Civile et al (2019), Civile, Cooke et al (2020), and Civile, Waguri et al (2020) however this time we introduced an additional condition. Specifically, we aimed to compare the face inversion effect when the tDCS procedure was administered only during the study phase (learning phase) vs. when it was delivered only during the recognition phase (test phase). Thus, we recruited three groups of participants randomly assigned to the three different experimental conditions. In the Anodal Study Phase group participants received the tDCS stimulation during the study phase only. This was the phase where participants were asked to memorize a set of upright and inverted faces. Following this, once the stimulation ended, participants were then engaged with the recognition task. In the Anodal Recognition Phase group, participants received no stimulation during the study phase. Instead, the stimulation started at the beginning of the recognition task and continued until the end. In the Sham group half of the participants were given the impression of being stimulated during the study phase, whereas the other half during the recognition phase.

#### Method

#### **Participants**

Overall, 72 naïve (right-handed) subjects (25 male, 47 Female; Mean age = 21.6 years, age range= 18-34, SD= 2.40) took part in the study. Participants were randomly assigned to either sham or the two anodal tDCS groups (24 in each group). They were all students from the University of Exeter selected according to the safety screening criteria approved by the Research Ethics Committee. The sample size was determined from earlier studies that used the same tDCS paradigm, behavioural design, face stimuli, and counterbalancing (Civile et al., 2018; Civile et al., 2019; Civile, Cooke et al., 2020; Civile, Waguri et al., 2020).

#### **Materials**

The study used a set of 256 face images standardized to grayscale on a black background (Civile, C, Elchlepp et al., 2018; Civile et al., 2018; Civile et al., 2019; Civile, Cooke et al., 2020, Civile, Waguri et al., 2020). All stimuli images were cropped so to remove distracting features such as hairline and adjusted for extreme differences in image luminance. The

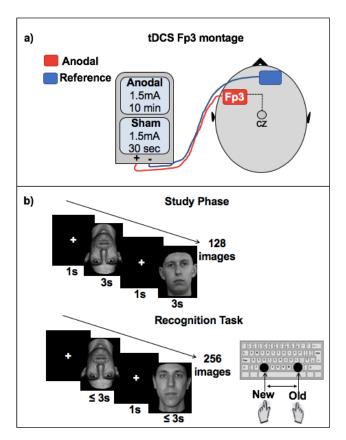
stimuli, whose dimensions were 5.63 cm x 7.84 cm, were presented at resolution of 1280 x 960 pixels. The experiment was run using Superlab 4.0.7b. on an iMac computer and the participants sat about 70 cm away from the screen.

#### The Behavioural Task

The experiment consisted of a 'study phase' and an 'old/new recognition phase' (Civile, McLaren, & McLaren, 2011; Civile et al., 2014; Civile et al., 2016; Civile et al., 2018; Civile et al., 2019; Civile, Cooke et al., 2020, Civile, Waguri et al 2020). In the study phase, participants were shown 64 upright and 64 inverted male and female faces for 128 stimuli in total (presented one at a time in random order). In the old/new recognition phase, 128 novel faces (half upright and half inverted) were showed intermixed with the 128 faces seen in the study phase, and all 256 stimuli were presented one at a time in random order. Participants responded according to whether or not they thought they had seen the face stimuli during the study phase. For a given participant, each face stimulus only appeared in one orientation during the experiment (see Figure 1, Panel b).

## The tDCS Paradigm

Stimulation was delivered by a battery driven constant current stimulator (neuroConn DC-Stimulator Plus) using a pair of surface sponge electrodes (7cm x 5cm i.e.35 cm<sup>2</sup>) soaked in saline solution and applied to the scalp at the target area of stimulation. We adopted the same tDCS montage used in Civile, Verbruggen et al (2016), Civile et al (2018), Civile et al (2019), Civile, Cooke et al (2020), Civile, Waguri et al (2020) (see Figure 1, Panel a). We adopted a bilateral bipolarnon-balanced montage with one of the electrodes (anode) placed over the target stimulation area (Fp3) and the other (cathode) on the forehead over the reference area (right eyebrow). The study was conducted using a double-blind procedure reliant on the neuroConn study mode in which the experimenter inputs numerical codes (provided by another experimenter), that switch the stimulation mode between "normal" (i.e. anodal) and "sham" stimulation. Participants were randomly assigned to one of the three tDCS condition groups.In the Anodal Study Phase group, a direct current stimulation of 1.5mA was delivered for 10 mins (5 s fade-in and 5 s fade-out) starting as soon as the subjects (n=24) began the study phase and finished before the old/new recognition task started. In the Anodal Recognition Phase group, the same direct current stimulation (1.5mA, for 10 mins with 5 s fadein and 5 s fade-out) was delivered starting as soon as the subjects (n=24) began the old/new recognition task and continuing throughout the study. In the Sham group, the identical stimulation mode was displayed on the stimulator and subjects experienced the same 5 s fade-in and 5 s fadeout, but with the stimulation intensity of 1.5mA delivered for just 30 s, following which a small current pulse (3 ms) was delivered every 550 ms (0.1mA over 15 ms) for the remainder of the 10 mins to check impedance levels. Half of the subjects (n=12) received the sham stimulation during the study phase only, whereas the other half (n=12) received it only during the old/new recognition task.



**Figure 1.** Panel a shows the tDCS montage used in the study. Panel b illustrates the old/new recognition task. In each trial of the study phase participants saw a fixation cross in the center of the screen, for 1 s, then a face image was presented for 3 s before moving on to the next trial. After all the 128 face stimuli had been presented, the program displayed a set of instructions, explaining the recognition task. During the recognition task, the faces were each shown for 3 s and participants pressed the '.' key if they recognized the face as having been shown in the study phase, or pressed 'x' if they did not (the keys were counterbalanced).

## Results

Following Civile et al (2018), Civile et al (2019), Civile, Cooke et al (2020), and Civile, Waguri et al (2020) the data from all the participants were used in the signal detection d' sensitivity analysis of the old/new recognition task (seen and not seen stimuli for each stimulus type) where a d' = of 0.00indicates chance-level performance (Stanislaw & Todorov, 1999). To calculate d', we used participants' hit rate (H), the proportion of YES trials to which the participant responded YES, and false alarm rate (F), the proportion of NO trials to which the participant responded YES. Intuitively, the best performance would maximize H (and thus minimize the Miss rate) and minimize F (and thus maximize the Correct Rejection rate); and thus, the larger the difference between H and F, the better is the participant's sensitivity. The statistic d' ("d-prime") is based on this difference; it is the distance between the Signal and the Signal + Noise. However, d' is not simply H-F; rather, it is the difference between the ztransforms of these 2 rates: d' = z(H) - z(F). We assessed performance against chance to show that all stimulus' conditions were recognized significantly above chance (for all conditions we found p < .01 for this analysis). Each p-value reported for the comparisons between conditions is two-tailed, and we also report the F or t value along with effect size  $(\eta^2_p)$ . We analyzed the reaction time (RT) data to check for any speed-accuracy trade-off. These analyses do not add anything to the interpretation of our results. For completeness, we give mean RTs for each of the stimulus' conditions: Sham Upright = 1195 ms; Sham Inverted = 1250 ms; Anodal Study Phase Upright = 1092 ms; Anodal Study Phase Inverted = 1142 ms; Anodal Recognition Phase Upright = 1175 ms; Anodal Recognition Phase Inverted = 1209 ms

We computed a 2 x 3 mixed model design using, as a within-subjects factor, *Face Orientation* (upright or inverted), and the between-subjects factor *tDCS Stimulation* (sham, anodal study phase, anodal recognition phase). Analysis of Variance (ANOVA) revealed a significant main effect of *Face Orientation*, F(1, 69) = 76.10, p < .001,  $\eta^2_p = .52$ , which confirmed that upright faces were better responded to than inverted ones. Importantly, a significant interaction between *Face Orientation* and *tDCS Stimulation* was found, F(1, 69) = 5.39, p = .007,  $\eta^2_p = .13$ . No main effect of *tDCS Stimulation* was found F(1, 69) = 2.06, p = .13,  $\eta^2_p = .05$ .

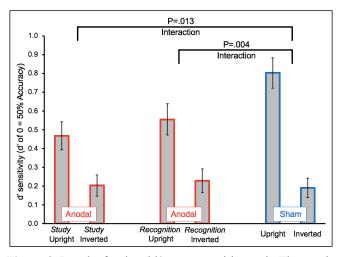
A 2 x 2 ANOVA using, as a within-subjects factor, *Face Orientation* (upright or inverted), and the between-subjects factor *Group* (sham, anodal study phase) revealed a significant interaction, F(1, 46) = 9.22, p = .004,  $\eta^2_p = .16$ . This was due to the inversion effect from the *sham* group, (M=.612, SE=.07), t(23) = 7.86, p < .001,  $\eta^2_p = .72$ , being larger than that in the *anodal Study Phase*, (M=.265, SE=.08), t(23) = 4.97, p = .004,  $\eta^2_p = .30$ .

A similar analysis comparing the inversion effect from the *Sham* group to that obtained in the *Anodal Recognition Phase* group, also revealed a significant interaction, F(1, 46) = 6.73, p = .013,  $\eta^2_p = .13$ . Again, the inversion effect in the *Sham* group was larger than that in the *Anodal Recognition Phase* group, (M=.327, SE=.07), t(23) = 4.22, p < .001,  $\eta^2_p = .43$  (see Figure 2).

Importantly, no interaction was found when we conducted a 2 x 2 ANOVA using, as a within-subjects factor, *Face Orientation* (upright or inverted), and the between-subjects factor Time of *tDCS Stimulation* (anodal study phase, anodal recognition phase)  $F(1, 46) = .297, p = .58, \eta^2_p = .01$ .

We compared the performance for upright faces in the three groups. This was done because, based on previous studies (Civile et al., 2018; Civile et al., 2019; Civile, Cooke et al., 2020 and Civile, Waguri et al., 2020) our specific tDCS procedure significantly affects only upright faces and not inverted ones. This analysis for the upright faces is also appropriate because the same stimulus sets are rotated across participants in a counterbalanced manner; so that each upright face seen in the *Sham* group for a given participant will equally often serve as an upright face for the participants in the *Anodal Study Phase* group and in the *Anodal Recognition Phase* group. There were statistically significant differences between group means for upright faces as determined by one-

way ANOVA, F(2, 69) = 4.741, p = .012. Performance for upright faces in the *Anodal Study Phase* group (M=.468, SE=.07) was significantly reduced compared to that in the *Sham* group (M=.803, SE=.08), t(23) = 2.87, p = .003,  $\eta^2_p = .26$ . A similar effect as found for upright faces in the *Anodal Recognition Phase* (M=.555, SE=.08) compared to *Sham*, t(23) = 1.84, p = .038,  $\eta^2_p = .13$ . No difference was found between upright faces in the *Anodal Study Phase* vs *Anodal Recognition Phase* groups, t(23) = .856, p = .44,  $\eta^2_p = .03$ . Finally, there were no statistically significant differences between group means for inverted faces as determined by oneway ANOVA, F(2, 69) = .110, p = .90.



**Figure 2.** Results for the old/new recognition task. The *x*-axis shows the stimulus conditions. The *y*-axis shows sensitivity d' measure. Error bars represent s.e.m.

# Additional Analysis: Anodal Recognition Phase group

To investigate further the *immediate* effect of the tDCS on the face inversion effect, we conducted an additional analysis where we split the data collected from the Anodal Recognition *Phase* group by first and second half of the recognition task. Hence, we computed a 2 x 2 ANOVA using, the withinsubjects factors, Face Orientation (upright or inverted), and Recognition Phase Halves (first half, second half). The results revealed a significant main effect of Face Orientation, F(1,23) = 7.92, p = .010,  $\eta^2_p = .25$ , which confirmed that upright faces were better responded to than inverted ones. No main effect of Recognition Phase Halves was found, F(1, 23) =2.88, p = .11,  $\eta^2_p = .11$ . Importantly, no significant interaction between Face Orientation and Recognition Phase Halves was found, F(1, 23) = .074, p = .78,  $\eta^2_p = .01$ , confirming that there was no difference between the inversion effect in the first half vs the second half of the recognition task.

# **General Discussion**

The tDCS procedure derived from a recent line of research developed by Civile, Verbruggen et al (2016), Civile et al (2018), Civile et al (2019), Civile, Cooke et al (2020), and Civile, Waguri et al (2020) is able to reduce the inversion effect for checkerboards (drawn from a prototype-defined

category that participants are familiar with) and the robust inversion effect usually found for faces. Critically, in both cases (for the checkerboards and the faces) anodal tDCS disrupted recognition of upright stimuli compared to sham. The overall results from the study reported here, confirmed that anodal tDCS at Fp3 induces a face recognition impairment in healthy students, in that they showed a reduced face inversion effect (compared to sham). And, once again, this was due to performance for upright faces in the anodal groups being reduced compared to sham. Importantly, because of the design of the study, we were able to directly compare the effect of anodal tDCS when delivered during the study phase (learning phase) vs when it was delivered during the recognition phase of the study. Hence, the key result from the study is that the face inversion effect was significantly reduced (compared to sham) in both anodal tDCS groups. Critically, in both groups the reduction of the inversion effect was due to impaired recognition performance for upright faces compared to that seen with sham stimulation. Given that the results from our study replicate (Anodal Study Phase group) and extend (Anodal Recognition Phase group) the line of research developed by Civile, Verbruggen et al (2016), Civile et al (2018), Civile et al (2019) and Civile, Cooke et al (2020), we interpret our results based on this literature and in terms of the MKM theory of perceptual learning (McLaren et al., 1989; McLaren and Mackintosh, 2000; McLaren, Forrest, & McLaren, 2012). This work is the first evidence that the tDCS procedure has an immediate effect on perceptual learning when applied. In fact, under normal (sham) conditions, by the end of the study phase participants were able to easily recognize the upright faces. However, this was not the case in the Anodal Recognition Phase group suggesting that the tDCS procedure is changing the way that faces are processed. The MKM model postulates that salience is modulated based on prediction error (i.e. past learning) and that this has an immediate impact on both learning and performance. The tDCS can be seen as preventing this error-based modulation of salience, resulting in enhanced generalization between exemplars, reducing the inversion effect because recognition performance for upright faces declines.

Normally, pre-exposure to prototype-defined categories of stimuli improves performance because it results in the unique features of an exemplar of that category (which help us discriminate between stimuli) being relatively more active during learning and performance compared to the common, prototypical features shared by the exemplars. This is a consequence of the common features shared by exemplars suffering from greater salience reduction than the unique ones because they are more predictable, and so more strongly associated to, by other elements present. One interpretation of the reduction of the inversion effect for checkerboards and that for faces is that the tDCS procedure induces a reconfiguration of the cognitive processing that develops representations of stimuli, such that instead of pre-exposure to a prototype-defined category enhancing the discriminability of the exemplars taken from that category, it instead now promotes generalization between them. This makes features common to those exemplars more prominent rather than

exaggerating exemplar differences. It is this change in perceptual learning that causes the reduction in the face inversion effect because it reduces individuals' ability to discriminate between and recognize different upright faces, which is normally enhanced by their expertise for face processing acquired via experience and manifesting as perceptual learning.

Perhaps the main impact of our findings relates to other possible explanations of the effect of the tDCS procedure that we use on face recognition, and on recognition of checkerboard exemplars taken from familiar categories. Because we had always previously given the tDCS during an early phase of the experiment, either during the study phase for faces or the categorisation phase for checkerboards, there was always the possibility that the neurostimulation was simply disrupting learning, and either directly hindering encoding of the to-be-remembered items (faces) or preventing familiarisation with the stimulus category (checkerboards). We now know that this cannot be the only mechanism at work here, because tDCS applied during the recognition phase after a lifetimes familiarisation with faces and after the encoding of them during the study phase still has the same impact on performance (recognition) as before. This is consistent with the MKM model predictions, because that model modulates the salience of stimulus representations online, and so can capture the immediate impact of our tDCS manipulation by simply stopping that modulation from occurring. But other explanations of expertise / perceptual learning, such as developing a larger representational space for encoding the stimuli as a result of encoding them, perhaps as a consequence of stimulus comparison during exposure to the stimuli, do not have this immediacy. We are encouraged by these results to think that our model of both perceptual learning and the effects of tDCS on it is a good one, and will continue to use it to guide future research on this phenomenon.

# Acknowledgments

This project has received funding from the Economic and Social Research Council *New Investigator Grant (Ref.ES/R005532)* awarded to Ciro Civile (PI) and I.P.L. McLaren (Co-I).

# References

Ambrus G., Zimmer M., Kincses Z., Harza I., Kovacs G., Paulus W., et al. (2011). The enhancement of cortical excitability over the DLPFC before and during training impairs categorization in the prototype distortion task. *Neuropsychologia* 49, 1974–1980.

Civile, C., Waguri, E., Quaglia, S., Wooster, B., Curtis, A., McLaren, R., Lavric, A., and McLaren, I.P.L. (2020). Testing the effects of transcranial Direct Current Stimulation (tDCS) on the Face Inversion Effect and the N170 Event-Related Potentials (ERPs) component. *Neuropsychologia*. doi: 10.1016/j.neuropsychologia.2020.107470

Civile, C., Cooke, A., Liu, X., McLaren, R., Elchlepp, H., Lavric, A., Milton, F., & I.P.L. McLaren. (2020). The effect of tDCS on recognition depends on stimulus generalization:

Neuro-stimulation can predictably enhance or reduce the face inversion effect. *Journal of Experimental Psychology: Animal Learning and Cognition*, 46, 83-98.

Civile, C., Obhi, S.S., & McLaren, I.P.L. (2019). The role of experience-based perceptual learning in the Face Inversion Effect. *Vision Research*, *157*, *84-88*.

Civile, C., McLaren, R., & McLaren, I.P.L. (2018). How we can change your mind: Anodal tDCS to Fp3 alters human stimulus representation and learning. *Neuropsychologia*, 119, 241-246.

Civile, C., Elchlepp, H., McLaren, R., Galang, C.M., Lavric, A., & McLaren, I.P.L. (2018). The effect of scrambling upright and inverted faces on the N170. *Quarterly Journal of Experimental Psychology*, 71, 2464-2476.

Civile, C., McLaren, R., & McLaren, I.P.L. (2016). The face inversion effect: Roles of first and second-order relational information. *The American Journal of Psychology*, 129,23-35.

Civile, C., Verbruggen, F., McLaren, R., Zhao, D., Ku, Y., & McLaren, I.P.L. (2016). Switching off perceptual learning: Anodal transcranial direct current stimulation (tDCS) at Fp3 eliminates perceptual learning in humans. *Journal of Experimental Psychology: Animal Learning and Cognition*, 42, 290-296.

Civile, C., Zhao, D., Ku, Y., Elchlepp, H., Lavric, A., & McLaren, I.P.L. (2014). Perceptual learning and inversion effect: Recognition of prototype-defined familiar checkerboards. *Journal of Experimental Psychology: Animal Learning and Cognition*, 40, 144-161.

Civile, C., McLaren, R., & McLaren, I.P.L. (2014). The face Inversion Effect-Parts and wholes: Individual features and their configurations. *Quarterly Journal of Experimental Psychology*, 67, 728-746.

Civile, C., McLaren, R. & McLaren, I.P.L. (2011). Perceptual learning and face recognition: Disruption of second-order relational information reduces the face inversion effect. In L. Carlson, C. Hoelscher, and T.F. Shipley (Eds.), *Proceedings of the 33<sup>rd</sup> Annual Conference of the Cognitive Science Society*, (pp. 2083-88). Cognitive Science Society.

Diamond, R. & Carey, S. (1986). Why faces are and are not special: An effect of expertise. *Journal of Experimental Psychology: General*, 115, 107-117.

Gauthier, I., & Tarr, M. (1997). Becoming a "Greeble" expert: exploring mechanisms for face recognition. *Vision Research*, *37*, *1673-1682*.

Gauthier, I., Williams, P., Tarr, M., & Tanaka, J. (1998). Training "greeble" experts: A framework for studying expert object recognition processes. *Vision Research*, *38*, 2401–28.

Haxby, J., Hoffman, E., & Gobbini, M. (2000). The distributed human neural system for face perception. *Trends in Cognitive Science*, *4*, 223–233.

Kincses, T., Antal, A., Nitsche, M., Bártfai, O., and Paulus, W. (2004). Facilitation of probabilistic classification learning by transcranial direct current stimulation of the prefrontal cortex in the human. *Neuropsychologia*, 42, 113–117.

McLaren, I.P.L., Kaye, H. & Mackintosh, N.J. (1989). An associative theory of the representation of stimuli: Applications to perceptual learning and latent inhibition. In R.G.M. Morris (Ed.) *Parallel Distributed Processing* -

Implications for Psychology and Neurobiology. Oxford, Oxford University Press.

McLaren, I.P.L. & Mackintosh, N.(2000). An elemental model of associative learning:Latent inhibition and perceptual learning. *Animal Learning and Behavior*, 38, 211-246.

McLaren, I.P.L., Forrest, C., & McLaren, R (2012). Elemental representation and configural mappings: combining elemental and configural theories of associative learning. *Learning and Behavior*, 40, 320-333.

McLaren, I.P.L., Carpenter, K., Civile, C., McLaren, R., Zhao, D., Ku, Y., Milton, F., and Verbruggen, F. (2016). Categorisation and Perceptual Learning: Why tDCS to Left DLPC enhances generalisation. *Associative Learning and Cognition*. Homage to Prof. N.J. Mackintosh. Trobalon, J.B., and Chamizo, V.D. (Eds.), University of Barcelona.

McLaren, I.P.L (1997). Categorization and perceptual learning: An analogue of the face inversion effect. *The Quarterly Journal of Experimental Psychology* 50, 257-273.

McLaren, I.P.L., and Civile, C. (2011). Perceptual learning for a familiar category under inversion: An analogue of face inversion? In L. Carlson, C. Hoelscher, & T.F. Shipley (Eds.), *Proceedings of the 33<sup>rd</sup> Annual Conference of the Cognitive Science Society*, (pp. 3320-25). Austin, TX: Cognitive Science Society.

Nitsche, M., Cohen, L., Wassermann, E., Priori, A., Lang, N., Antal, A., and Pascual-Leone, A. (2008). Transcranial direct current stimulation: state of the art 2008. *Brain Stimulation*, 1, 206–223.

Radman, T., Ramos, R.L., Brumberg, J.C., and Bikson, M. (2009). Role of cortical cell type and morphology in subthreshold and suprathreshold uniform electric field stimulation in vitro. *Brain Stimulation 2*, 215–228.

Robbins R, and McKone E. (2007). No face-like processing for objects-of-expertise in three behavioural tasks. *Cognition*, 103, 34–79.

Scapinello, K. & Yarmey, D.(1970). The role of familiarity and orientation in immediate and delayed recognition of pictorial stimuli. *Psychonomic Science*, 21, 329-330.

Stanislaw H, Todorov N. 1999. Calculation of signal detection theory measures. *Behavior Research Methods Instruments & Computers* 31, 137-149.

Tanaka, J. W., & Farah, M. J. (1991). Second-order relational properties and the inversion effect: Testing a theory of face perception. *Perception & Psychophysics*, 50, 367–372.

Valentine, T., & Bruce, V. (1986). Mental rotation of faces. *Memory & Cognition*, 16, 556–566.

Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, 81, 141-145.

Yovel G., & Kanwisher N.(2005). The neural basis of the behavioral face-inversion effect *Current Biology*, 15,2256-62.