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Using transcranial Direct Current Stimulation (tDCS) to modulate the face inversion effect on the N170 ERP component.

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Abstract

In the present study, we combined tDCS and EEG to examine the electrophysiological responses to the tDCS-induced effects on the face inversion effect showed in recent studies. A double-blind procedure with a between-subjects design (n=48) was used with the subjects, recruited from the student population, being randomly assigned to either tDCS anodal or sham condition. The tDCS stimulation was delivered over the DLPFC at Fp3 site for 10 min at an intensity of 1.5mA while subjects engaged in an old/new recognition task traditionally used to obtain the inversion effect. The behavioural results generally confirmed previous findings. Critically, the results from the N170 show an effect of tDCS. Specifically, the tDCS procedure was able to modulate the N170 peak component by reducing the inversion effect on the latencies (i.e. less delay between upright and inverted faces) and by increasing the inversion effect on the amplitudes (i.e. larger N170 for inverted vs upright faces). We interpret the results based on the previous literature in regard to the inversion effect on the N170 component.

Keywords: Inversion effect; tDCS; N170, perceptual learning

Introduction

Several researchers have studied the nature of face recognition skills by investigating the causes of a robust phenomenon known as the face inversion effect. This refers to reduced performance when we try to recognize familiar faces turned upside down (Yin, 1969). When it was first discovered this phenomenon was used as a marker for "specificity" of face processing. This was because the inversion effect was found to be larger for faces than for other visual stimuli such as houses or planes (Valentine & Bruce, 1986; Yovel & Kanwisher, 2005). However, Diamond and Carey's (1986) finding of a large inversion effect for dog images when participants were dog breeders (vs that exhibited by novices), and Gauthier's work on perceptual expertise and the inversion effect for novel categories of objects named Greebles (Gauthier & Tarr, 1997) challenged the idea that faces are special and introduced "expertise" as a contributing factor to the inversion effect. Importantly, in 1997, McLaren using a set of artificial stimuli, checkerboards (so that expertise can be fully controlled), reported the first evidence of an inversion effect for novel stimuli that was predicted based on a specific model of perceptual learning, the MKM model (McLaren, Kave & Mackintosh, 1989; McLaren & Mackintosh, 2000). Following this, Civile et al. (2014) extended McLaren's findings to the type of *old/new recognition task* originally used to investigate the face inversion effect (e.g. Yin, 1969). Taken together, Gauthier and Tarr's (1997), McLaren's (1997), and Civile et al's (2014) studies provide support for the Diamond and Carey's (1986) expertise account of face recognition; they have also served as a basis for further investigations of face and object recognition using Electroencephalogram (EEG) derived event-related potentials (ERPs).

Early studies on face recognition claimed the N170 ERP component to be the neural signature for face stimuli (Bentin et al., 1996). The N170 is a negative-polarity ERP deflection (peak) maximal at 140-200ms usually found at occipitaltemporal electrodes after a face stimulus is presented (Bentin et al., 1996; George et al., 1996). The N170 has been found to be larger in amplitude and delayed in latency for inverted faces compared to upright faces. This is what has been commonly defined as the inversion effect on the N170 (Eimer, 2000). Rossion et al (2002) directly compared the N170 for faces and Greebles demonstrating how after the

training phase with upright Greebles, the inversion effect (i.e. delayed and larger amplitude for inverted stimuli) was of a similar magnitude for both faces and Greebles. In a similar vein, Busey and Vanderkolk (2005) showed that fingerprint experts exhibited an inversion effect on the N170 (similar to that for faces) in response to images of fingerprints. Furthermore, Civile et al. (2014a, Exp. 4), found an inversion effect on the N170 for checkerboards drawn from a familiar prototype-defined category (a larger and delayed N170 for inverted checkerboards compared to upright ones). The results from these studies provided motivation for a departure from the original account of the N170 component as being specific to faces, toward a position where the inversion-induced enhancement and delay of the N170 can be obtained for non-face categories of stimuli if they are made sufficiently familiar.

In recent years, Civile et al (2016) first, and then Civile, McLaren, and McLaren (2018a) (for a pilot see also Civile, Obhi & McLaren, 2018b) strengthened the analogy between the inversion effect for checkerboards (Civile et al., 2014), and that for faces, through demonstrating that they both share the same causal mechanism. Using a specific tDCS paradigm, the authors were able to modulate perceptual learning and selectively affect the robust inversion effect that otherwise would have been obtained for checkerboards and face stimuli. Anodal tDCS delivered over the DLPFC at Fp3 site (see Ambrus et al., 2011 for an example of previous studies targeting the same brain area to modulate categorization for prototype-defined stimuli) for 10 mins at an intensity of 1.5mA eliminated the inversion effect found for checkerboards by reducing performance for upright checkerboards taken from a familiar category (compared to controls) (Civile et al., 2016). Critically, the same tDCS paradigm is also able to reduce the robust face inversion effect by affecting recognition performance for upright faces (Exp.1 and the replication Exp.2 in Civile et al., 2018a). Furthermore, through an active control study the authors showed that applying the same tDCS anodal stimulation on a different brain area did not result in any difference between the face inversion effect compared to the sham group (Exp.3, Civile et al., 2018a). Overall the results from these studies using tDCS show how a particular tDCS procedure can modulate perceptual learning and so reduce the robust inversion effect that would otherwise be obtained with checkerboards (after participants have gained enough expertise with them) or faces.

In the present study, we extended the tDCS procedure adopted by Civile et al (2016) and Civile et al (2018a) to the face inversion effect on the N170 ERP component. To our knowledge, this is the first study that attempts to examine the behavioural tDCS-induced effects on the inversion effect to electrophysiological responses on the N170. Showing that the tDCS procedure used to affect the inversion effect for checkerboards and for faces can also modulate the N170, would strengthen the link between perceptual learning (and in general the expertise account) and face reocognition.

Method

Subjects

Overall, 48 naïve (right-handed) subjects (18 male, 30 Female; Mean age = 21.3 years, age range= 18-27, SD= 2.25) took part in the study. Subjects were randomly assigned to either sham or anodal tDCS groups (24 in each group). All the subjects were students from the University of Exeter and were selected according to the safety screening criteria approved by the Research Ethics Committee at the University of Exeter. The sample size was determined from earlier studies that used the same tDCS paradigm, EEG paradigm, face stimuli, and counterbalancing (Civile et al., 2018a, b, c).

Materials

The study used a set of 256 face images standardized to grayscale on a black background (Civile et al., 2018a, b, c). All stimuli images were cropped removing 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. Examples of the stimuli used are given in Figure 1. The experiment was run using E-prime software Version 1.1 installed on a PC computer.

The Behavioural Task

The experiment consisted of a 'study phase' and an 'old/new recognition phase' (Civile et al., 2018a,b,c).

Study Phase. Once subjects gave their consent, the instructions for the Study Phase were presented on the screen. The aim of the task was for the subjects to try to memorize the faces presented on the screen. The trial started with a fixation cross (500ms) in the center of the screen, immediately followed by a blank screen (500ms), and then by a facial stimulus (3000ms). Then the fixation cross and the black screen were repeated, and another face presented, until all stimuli had been presented. Overall, 128 face stimuli were presented inverted. After all the 128 face stimuli had been presented, the program displayed another set of instructions, explaining the recognition task.

Recognition Task. In this task, subjects were asked to press the 'z' key if they recognized the face stimulus as having been shown in the study phase on any given trial, or press 'm' if they did not (the keys were counterbalanced). All the stimuli previously seen in the study phase were presented again, "old", intermixed with 128 "new" faces split by the two conditions (upright and inverted). All the faces were presented one at a time at random order. The trial structure was as that in the study phase however this time the stimuli were presented for a longer period (4000ms).

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 cm²) soaked in saline solution and applied to the scalp at the target area of stimulation. We adopted the same tDCS montage used in Civile et al (2018a)'s study (Exp. 1 & 2). Hence, one of the electrodes (anode) was 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 otherwise unconnected with running the experiment), that switch the stimulation mode between "normal" (i.e. anodal) and "sham" stimulation. In the anodal condition, 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 began the behavioral 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 fade-out, 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. Subjects were randomly assigned to one of the tDCS groups (Sham or Anodal). For every subject the stimulation started at the beginning of the Study Phase and finished before the Old/New Recognition Task started.

Given the novelty inherent in combining tDCS and EEG techniques, especially with using two separate pieces of equipment, it is worth noting some of the practical challenges faced during the implementation of the study. Specifically, we realised the tDCS stimulation (both sham and anodal) induced strong artefacts on the EEG data. Thus, we made sure that the tDCS stimulation ended by the end of the study phase before we started recording the EEG for the recognition phase. Hence, our analysis of the EEG data will be entirely for the recognition phase.

EEG Recordings

The EEG was sampled at 1000 Hz, with a band-pass of 0.016-100 Hz, the reference at Cz and the ground at AFz using 32 Ag/AgCl active electrodes and BrainAmp amplifiers. The electrodes were placed on the scalp in an extended 10-20 configuration plus one on each earlobe (references during online recording). Their impedances were kept below 10 k Ω .

Data Processing and Analysis

As mentioned above in the *tDCS Paradigm* section the ERP analysis was limited to the recognition phase. Data processing was performed in BrainVision Analyzer. The data was first filtered offline using a Butterworth Zero Phase filter with a low cutoff of 0.5 Hz and a high cutoff of 30 Hz, each with a 24 dB/oct slope. Individual channels were manually inspected and removed from further analysis where physical interference from a tDCS electrode was noted during set-up, or where data otherwise showed signs of significant artefacts throughout. Electrodes retained the online reference to Cz. Peak amplitudes of the N170 were examined for differences between the experimental conditions. To improve the

estimates of the amplitude and latency the N170 extraction was aided by linear decomposition of the EEG using Independent Component Analysis (ICA, Bell & Sejnowski, 1995). The ICA was run separately for each subject using all scalp channels and the entire dataset. The EEG segments were then averaged for every participant and experimental condition. For each subject, we identified ICA components that: (1) showed a deflection (peak) in the N170 time-range (at 160-220 ms following stimulus onset), and (2) had a scalp distribution containing an occipital-temporal negativity characteristic of N170 (the scalp distributions of components are the columns of the inverted unmixing matrix). This resulted in 1-4 ICA components corresponding to the N170 identified in most subjects - these were back-transformed into the EEG electrode space (by multiplying the components with the inverted unmixing matrix that had the columns corresponding to other components set to zero) and submitted to statistical analysis of N170 peak amplitude and latency. N170 latency and amplitude analyses were restricted to electrode PO8, (over the right temporal hemisphere) which often in the literature has shown bigger effects on the N170 (Civile et al., 2018c; Civile et al., 2014; Civile et al., 2012; Rossion & Jacques, 2008).

Results

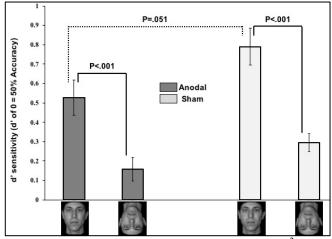
Behavioral Results

Following Civile et al (2018a,b,c) the data from all the participants were used in the signal detection d' sensitivity analysis of the recognition task (seen and not seen stimuli for each stimulus type) where a d' = of 0.00 indicates chancelevel performance (Stanislaw & Todorov, 1999). We assessed performance against chance to show that both upright and inverted face stimuli in both the tDCS sham and anodal groups across the three experiments were recognized significantly above chance (for Sham Inverted, Sham Upright and Anodal Upright we found p < .001 for this analysis, for Anodal Inverted we found p = .016). Each pvalue reported for the comparisons between conditions is two-tailed, and we also report the F or t value along with effect size. We also analyzed the reaction times (RTs) data to check for any speed-accuracy trade-off. We do not report this analysis here because it does not add anything to the interpretation of our results. For completeness, we give mean RTs for each of the stimulus' conditions: Sham Upright = 1240 ms; Sham Inverted = 1277 ms; Anodal Upright = 1263 ms; Anodal Inverted = 1267 ms.

d-Prime Analysis

We computed a 2 x 2 mixed model design using, as a within-subjects factor, *Face Orientation* (upright or inverted), and the between-subjects factor *tDCS Stimulation* (sham or anodal). Based on previous studies (Civile et al., 2018a,b) we expected the inversion effect for the anodal group to be smaller than that in the sham group. Analysis of Variance (ANOVA) revealed that numerically this was case but this time the interaction was not statistically significant, F(1, 46) = .947, p = .33, $\eta^2_p = .02$. There was a significant

main effect of *Orientation* F(1, 46) = 43.95, p < .001, $\eta^2_p =$.48, which confirmed that upright faces were better responded to than inverted ones. A main effect of tDCS Stimulation was found with performance in the anodal stimulation (M=.343, SE=.06) being significantly reduced compared to that in sham group (M=.542, SE=.05), F(1, 46) = 5.39, p = .025, $\eta^2_p = .10$. Paired t test analyses were conducted to compare performance on upright and inverted face stimuli (the inversion effect) in each tDCS group (sham, anodal). Based on previous studies that used the same stimuli and tDCS paradigm (Civile et al., 2018a,b) our primary measure was the face inversion effect given by comparing performance on upright and inverted faces in each tDCS group. We also directly compared the performance for upright faces in the sham vs tDCS group. This is particularly appropriate because the same stimulus sets are rotated across participants in a counterbalanced manner; so that each upright face seen in the anodal group for a given participant will equally often serve as an upright face for the participants in the sham group. A significant inversion effect was found in the sham group (M=.495, SE=.10), t(23) = 4.97, p < .001, η^2_p = .38, and a numerically reduced inversion effect was found in the tDCS anodal group (M=.368, SE=.07), t(23) =4.62, p < .001, $\eta^2_p = .25$ (see Figure 1). Recognition for upright face stimuli in the anodal group was lower compared



to that in the sham group, t(46) = 2.05, p = .051, $\eta^2_p = .19$. We also found a trend towards performance for inverted faces being reduced in the anodal relative to the sham group, t(46) = 1.81, p = .083, $\eta^2_p = .16$.

Figure 1. 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.

Bayes Factor Analysis

Because we did not find a significant interaction in this experiment, as we had expected, we performed Bayesian analyses to check that our results fell within the usual parameters of our previous work. Using the procedure outlined by Dienes (2011), we first conducted a Bayes analysis on the Face Orientation by Stimulation interaction. Thus, we used the interaction effect averaged over Experiments 1 and 2 (0.30) from Civile et al. (2018a; same tDCS procedure, behavioural paradigm, stimuli, and sample size as in the study here reported)'s work as the prior (standard deviation of p). Then we used the standard error (0.03) and mean difference (0.13) for the interaction in our study, assumed a one-tailed distribution for our theory, and gave it a mean of 0. This resulted in a Bayes factor of 2162.84, which is strong evidence (greater than 10, for the conventional cut-offs see Jeffrey, 1961 and Dienes, 2011) indeed for the theory, in this case that the interaction will be positive and non-zero. Next, because in Civile et al. (2018a) both Experiments 1 & 2 had performance for the upright faces significantly better in the sham group compared to that in the anodal group, we calculated the Bayes factor for this effect in our study using as the prior the difference between sham minus anodal upright faces averaged over Civile et al. (2018a)'s Experiments 1 & 2 (0.28). We then used the standard error (0.11) and mean difference (0.26) between sham upright faces minus anodal upright faces in our study and assumed a one-tailed distribution for our theory with a mean of 0. This gave a Bayes factor of 8.10, which provides good evidence (as greater than 3) that sham performance on upright faces is higher than that under tDCS.

N170 ERP Results

In analyzing the N170 peak component we computed the same statistical analyses as for the behavioral data.

N170 Peak Latency Analysis

A 2 x 2 repeated measure ANOVA revealed a trend towards a significant interaction for peak latency, F(1,46) =3.26, p = .077, $\eta_p^2 = .06$. A significant main effect of *Orientation* was found, F(1, 46) = 51.19, p < .001, $\eta_p^2 = .52$. No main effect of *tDCS Stimulation* was found, F(1, 46) =.077, p = .783, $\eta_p^2 = .00$. A significant inversion effect (i.e. a delayed N170 peak for inverted vs upright faces) was found in the sham group (M=7.95ms, SE=1.28), t(23) = 6.20, p <.001, $\eta_p^2 = .62$, and a numerically reduced inversion effect was found in the tDCS anodal group (M=4.70ms, SE=1.22), t(23) = 3.86, p < .001, $\eta_p^2 = .39$. No difference was found between the N170 latencies for upright stimuli in the anodal vs sham group, t(46) = .235, p = .815, $\eta_p^2 = .00$. No significant difference was found between inverted faces in the anodal vs sham group, t(46) = .903, p = .375, $\eta_p^2 = .04$.

N170 Peak Amplitude Analysis

A 2 x 2 ANOVA revealed a significant Orientation by Stimulation interaction for peak amplitude, F(1,46) = 4.06, p = .049, $\eta^2_p = .09$, and a main effect of Orientation, F(1, 46) = 45.47, p < .001, $\eta^2_p = .49$. No main effect of tDCS Stimulation was found, F(1, 46) = .178, p = .679, $\eta^2_p = .00$. Contrarily to what we found for N170 latencies, the inversion effect (larger N170 for inverted vs upright faces) was found to be larger in amplitude in the anodal group (M=3.32µV, SE=.63) t(23) = 5.22, p < .001, $\eta^2_p = .54$, compared to that found in the sham group (M=2.41, SE=.52) t(23) = 4.32, p < .001, $\eta^2_p = .44$ (see Figure 2). No difference was found between the N170 amplitude for upright stimuli in the anodal vs sham group, t(46) = .033, p = .975, $\eta^2_p = .00$. Despite a numerically larger N170 for the inverted faces in the anodal vs sham group, no significant difference was found, t(46) = .882, p = .386, $\eta^2_p = .03$.

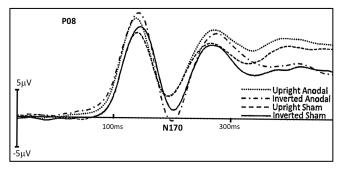


Figure 2. Waveforms at electrode P08 for the four conditions. The X axis shows the elapsed time after a stimulus was presented. The Y axis gives the amplitudes (μV) of the ERPs in the recognition phase of the experiment.

General Discussion

In the study reported here we examined the effects of tDCS on electrophysiological correlates of the face inversion effect. Specifically, we adopted the same tDCS procedure used by Civile et al (2018a,b) and Civile et al (2016) to modulate perceptual learning and affect the inversion effect for newly acquired stimuli (i.e. checkerboards) and longterm learnt stimuli i.e. faces. Our behavioral results are in line with previous work. Despite the inversion effect in the anodal group being only numerically reduced compared to sham, the additional Bayes Factor analysis gives us confidence that our effects are in line with previous work (Civile et al., 2018a). Importantly, as in previous studies, we find that anodal tDCS is particularly effective in reducing the recognition performance for upright faces, a result also supported by the Bayes Factor analysis. Our behavioral results also hint at a tendency (not significant) for anodal tDCS to reduce performance for the inverted faces. This is a new trend that previous studies (Civile et al., 2018a,b) did not show.

The most novel aspect of the present study involves the ERP results. To our knowledge, the current study provides the first evidence for tDCS being able to modulate a robust ERP component such as the N170 often associated with faces as well as sets of prototype-defined artificial stimuli that participants have become familiar with (Rossion et al., 2002; Civile et al., 2014). Intriguingly, our results suggest a dissociation of the effects that tDCS has on the N170. Specifically, in the latencies we find tDCS reduces the inversion effect compared to sham (less delay between the peaks for inverted vs upright faces). At the same time, tDCS increases the inversion effect on the N170 amplitudes compared to sham (a larger difference between the peak amplitude of the N170 for inverted vs upright faces). The effects of tDCS on the N170 latencies are more easily interpreted. Specifically, on the expertise account we can argue that a delayed N170 is recorded for a target face or familiar stimulus as a consequence of the familiarity lost when the target stimulus is turned upside down. We know from the behavioral results that anodal tDCS affects perceptual learning (by reducing expertise) for upright faces, making them more similar to stimuli drawn from an unfamiliar category, and thus this would result in a latency more similar to that for inverted faces.

Remarkably, the results from the N170 amplitude analysis provide some evidence for a dissociation from the tDCS-induced effects on the ERP latencies. Here anodal tDCS increased the inversion effect seen in the N170 amplitudes, and the inverted faces in this condition were found to elicit the largest N170 (i.e. more negative) compared to all the other stimulus conditions. But we should beware of attributing this effect to the impact of tDCS on the inverted faces, as this wasn't independently significant. All we can be sure of is that the inversion effect (difference between peak amplitudes) increased as a result of tDCS. In line with our explanation for the N170 latencies, if we assume that anodal tDCS is affecting participant's expertise for faces, then why would this have any impact on inverted faces when we have already argued that it will affect upright ones? Instead, it may be better to just focus on the significant effect (i.e. the difference between upright and inverted), and speculate that there may be some shift in baseline effects in our tDCS condition (not unlikely, we are, after all, activating a substantial region of frontal cortex using anodal stimulation) that results in the inverted face ERP apparently showing the greatest effect.

That still leaves us with the effect on peak amplitude to explain, and here it may be that we have to appeal to the difference between upright faces, for which we have expertise, and two different types of stimuli for which we do not. We assume that inverted faces do not benefit from our expertise with upright faces, whilst still acknowledging that they are readily recognized as faces. Another type of stimulus that would not benefit from expertise would be an entirely novel stimulus (a Greeble, a checkerboard). But this stimulus is not an inverted face. Now, if we postulate that tDCS makes the upright faces more like a novel stimulus, and that novel stimuli, other things being equal, do not show such a pronounced N170, then the greater difference from the inverted face N170 could be explained. Essentially, we would argue that tDCS shifts the upright face N170 towards that of a novel stimulus, which has a smaller amplitude and a greater latency, and that this is why we get our apparently 'opposite" effects.

Interestingly, something like this pattern of results has previously been found in EEG studies where the level of familiarity for the stimuli presented was manipulated directly by means of training to the stimuli or by altering the typical familiar stimulus configuration (e.g. rearrange the locations of the features within a face). In Civile et al. (2014)'s study, the N170 peak amplitudes for inverted checkerboards taken from a familiar category were larger compared to the other conditions (upright checkerboards from a familiar category and upright and inverted novel checkerboards). Furthermore, Civile et al (2018c) found normal inverted faces elicited a larger N170 amplitude compared to normal upright faces and scrambled (i.e. the facial features were shuffled) upright/inverted faces (see also Civile et al., 2012 for similar results using Thatcherised faces). Finally, also Rossion et al. (2002) showed (in the pre-training phase) the N170 peak amplitude being larger for normal inverted faces compared to normal upright faces, and upright/inverted Greebles. Civile et al (2018c) suggested that this effect is due to the fact that the normal inverted faces possess all the configural information (spatial relations) of a normal upright face, but presented in an orientation that not only makes it difficult to make use of them but imposes an additional cost. Thus the idea here would be that the differences in the N170 caused by inversion only partly index the effect of perceptual learning (in the latencies), the amplitude difference reflects something else (perceptual effort perhaps).

In conclusion, in the study reported here, we have provided some evidence in support of a tDCS procedure able to modulate the face inversion of the N170 component. Importantly, the tDCS-induced effects on the N170 seem to dissociate between latencies and amplitudes of the N170. Further studies will be needed to establish these effects.

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References

Ambrus G. G., Zimmer M., Kincses Z. T., 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.

Bell, A. J, & Sejnowski, T. J. (1995). An informationmaximization approach to blind separation and blind deconvolution. *Neural Computation*, 7, 1129-59.

Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neurosci*ence, 8, 551-565.

Busey, T., & Vanderkolk, J. (2005). Behavioural and electrophysiological evidence for configural processing in fingerprint experts. *Vision Research*, 45, 431-448.

Civile, C., Elchlepp, H., McLaren, R., Lavric, A & McLaren, I.P.L. (2012). Face recognition and brain potentials: Disruption of configural information reduces the face inversion effect. *Proceedings of the 34th Annual Conference of the Cognitive Science Society,* (pp. 1422-27). Austin, TX: Cognitive Science Society.

Civile, C., Zhao, D., Ku, Y., Elchlepp, H., Lavric, A., & McLaren, I.P.L. (2014). Perceptual learning and inversion effects: Recognition of prototype-defined familiar checkerboards. *Journal of Experimental Psychology: Animal Behavior Processes*, 40, 144-61.

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

Civile, C., Obhi, S.S., & McLaren, I.P.L. (2018b). The Role of Experience Based Perceptual Learning in the Face Inversion Effect. *Vision Research*, doi.org/10.1016/j.visres.2018.02.010.

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

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

Dienes, Z. (2011). Bayesian versus orthodox statistics: Which side are you on? *Perspectives on Psychological Science*, 6, 274–290.

Eimer, M. (2000). The face-specific N170 component reflects late stages in the structural encoding of faces. *NeuroReport*, 11, 2319-2324.

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

McLaren, I.P.L (1997). Categorization and perceptual learning: An analogue of the face inversion effect. *The Quarterly Journal of ExperimentalPsychology 50A (2),* 257-273.

George, N., Evans, J., Fiori, N., Davidoff, J., & Renualt, B. (1996). Brain events related to normal and moderately scrambled faces. *Cognitive Brain Research*, 4, 65-76.

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.J. (2000). An elemental model of associative learning: Latent inhibition and perceptual learning. *Animal Learning and Behavior*, 38, 211-246.

Rossion, B., Gauthier, I., Goffaux, V., Tarr, M.-J., Crommelinck, M. (2002). Expertise training with novel objects leads to face-like electrophysiological responses. *Psychological Science*, 13, 250-257.

Rossion B. & Jacques C. (2008). Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain Ten lessons on the N170. *Neuroimage*, 39, 1959–1979.

Valentine, T., & Bruce, V. (1986). Recognizing familiar faces : The role of distinctiveness and familiarity. *Canadian Journal of Psychology*, 40, 300-305.

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.