Please cite as:

Civile, C., Cooke, A., Liu, X., McLaren, R., Elchlepp, H., Lavric, A., Milton, F., and I.P.L. McLaren. (in press). 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*.

The Effect of tDCS on Recognition Depends on Stimulus Generalization: Neuro-stimulation can predictably *enhance* or *reduce* the face inversion effect

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Abstract

This paper reports results from three experiments that investigate how a particular neuro-stimulation procedure is able, in certain circumstances, to selectively increase the face inversion effect by enhancing recognition for upright faces, and argues that these effects can be understood in terms of the MKM theory of stimulus representation. We demonstrate how a specific transcranial Direct Current Stimulation (tDCS) methodology can improve performance in circumstances where *error-based salience modulation* is making face recognition harder. The three experiments used an *old/new recognition* task involving sets of normal vs Thatcherised faces. The main characteristic of Thatcherised faces is that the eyes and the mouth are upside down, thus emphasizing features that tend to be common to other Thatcherised faces and so leading to stronger generalization making recognition worse. Experiment 1 combined a behavioural and ERP study looking at the N170 peak component, which helped us to calibrate the set of face stimuli needed for subsequent experiments. In Experiment 2 we used our tDCS procedure (between-subjects and double-blind) in an attempt to reduce the negative effects induced by error-based modulation of salience on recognition of upright Thatcherised faces. Results largely confirmed our predictions. In addition, they showed a significant improvement on recognition performance for upright normal faces. Experiment 3 provides the first direct evidence in a single study that the same tDCS procedure is able to both *enhance* performance when normal faces are presented with Thatcherised faces, and to *reduce* performance when normal faces are presented with other normal faces (i.e. male vs female faces). We interpret our results by analyzing how salience modulation influences generalization between similar categories of stimuli.

Key Words: Perceptual learning; Generalization; tDCS; Inversion Effect; Face Recognition

Background

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 the 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 the "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; Valentine 1988; Yovel & Kanwisher, 2005). However, Diamond and Carey's (1986) finding of a large inversion effect for dog images when participants were dog breeders (as distinct from 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. At the same time, McLaren (1997), using a set of checkerboard stimuli that constituted an artificial, prototype-defined category (so that expertise could be fully controlled), reported the first evidence of an inversion effect for novel stimuli that were quite unlike faces. This result had been predicted by a theory of perceptual learning, the MKM model (McLaren, Kaye and Mackintosh, 1989; McLaren and Mackintosh, 2000; McLaren, Forrest and McLaren, 2012). Some years later, Civile, Zhao, Ku, Elchlepp, Lavric, and McLaren, (2014a) extended McLaren's findings by demonstrating a similar result using an *old/new recognition task* of the type originally employed to investigate the face inversion effect (e.g. Yin, 1969).

In more recent studies, Civile, Verbruggen, McLaren, Zhao, Ku, and McLaren, (2016a), Civile, McLaren and McLaren (2018a) and Civile, Obhi, and McLaren (2019) have strengthened the analogy between the inversion effect for checkerboards (Civile et al., 2014a), which we now use as our index of perceptual learning, and that for faces, by demonstrating that they both share the same causal mechanism. Using a non-invasive neuro-stimulation technique, the authors were able to modulate perceptual learning and thus selectively affect the robust inversion effect that otherwise would have been obtained for both checkerboards and face stimuli.

The specific neuro-stimulation technique used is known as transcranial Direct Current Stimulation (tDCS). In the set-up employed for these experiments, tDCS consists of placing two electrodes (i.e. the target and the reference) on the scalp and administering a low current as stimulation (in most studies between 1-2mA) through them (Nitsche et al., 2008). When *anodal* stimulation is delivered, the current is intended to cause a depolarization of the resting membrane potential (i.e. the stable value of the electric potential between interior and exterior of a cell), which modulates neural excitability. *Sham* (control) stimulation lasts for a brief time. With this last procedure, participants do not realize they are not receiving prolonged continuous stimulation (Radman, Ramos, Brumberg & Bikson, 2009).

Ambrus et al (2011) provided evidence for anodal tDCS delivered over the left DLPFC at Fp3 site influencing categorization learning for sets of prototype-defined stimuli (pattern configurations). The DLPFC region was chosen in their experiment because of previous fMRI studies showing this region of the brain was activated during category learning tasks. The Fp3 area was selected because of being particularly implicated in participants with high categorization performance (Seger et al., 2000; Ambrus et al, 2011). Ambrus et al (2011) specifically showed how anodal tDCS was able to eliminate the prototype effect (better categorization performance for non-pre-exposed category prototypes compared to category exemplars) by significantly reducing participants' performance at identifying prototype and low distortion pattern exemplars as category members compared to sham (see Kincses et al, 2013 for another example of the same tDCS montage applied on categorization learning tasks).

Civile et al (2016a) extended the same tDCS montage adopted by Ambrus et al (2011) to the same old/new recognition task for prototype-defined categories of checkerboards developed by Civile et al (2014a). The authors showed that anodal stimulation, compared to sham, (applied for 10 mins at 1.5 mA intensity at the Fp3 brain site) can significantly reduce the inversion effect that would normally be obtained for sets of familiar prototype-defined chequerboards (McLaren, 1997; McLaren & Civile 2011; Civile et al., 2014a). Importantly, recognition performance for upright familiar checkboards was reduced by the anodal stimulation compared to sham. Following this, Civile et al (2018a) and Civile et al (2019) tested the tDCS procedure on the inversion effect for faces. The authors were able to show how the same tDCS procedure that affected the inversion effect for checkerboards also significantly reduced the commonly observed inversion effect for faces. Critically, the recognition performance for upright faces was reduced by the anodal stimulation compared to sham. These results are particularly important because the face inversion effect is one of the most robust phenomena in cognitive psychology, one that has been demonstrated many times, and is even a mainstay of undergraduate practical classes. To be able to reliably diminish this effect, using a neuro-stimulation technique under double-blind conditions as Civile et al (2018a) have done means that we have a technique that can influence one of the key "markers" for learning and memory in humans. One challenge addressed here, then, is to try to establish exactly what this technique is doing.

Civile et al (2018a) and Civile et al (2019)'s studies showed how the reduction of the inversion effect seemed to be mainly due to the disruptive effect that anodal tDCS (compared to sham) had on recognition performance for upright faces rather than the inverted ones (Civile et al

2016a showed a similar effect with checkerboards drawn from a familiar category). Thus, the authors offered an analysis of the effects obtained in terms of a reduction in perceptual learning (i.e. expertise) for stimuli from a very familiar category like faces. The idea is that the tDCS procedure affects individuals' ability to discriminate between faces, specifically by reducing the advantage enjoyed by upright faces relative to inverted ones in a standard old/new recognition task. Civile et al (2018a) and Civile et al (2019) described the effects of the tDCS procedure as a reconfiguration of the processing that produces representations of stimuli. Instead of pre-exposure to a prototype-defined category enhancing the discriminability of exemplars taken from that category (i.e. leading to perceptual learning) it now enhances generalization between them and makes the common features of those exemplars more prominent, rather than enhancing the relative salience of the unique features that constitute their differences. As a consequence of this, the authors made the case for tDCS in these circumstances actually changing the way people process faces, rather than simply making them worse at it. Thus, if we hypothesize that the tDCS procedure is changing the way that people process faces, not just simply making them worse at face recognition in some way, then we should be able to find circumstances in which this change leads to better, rather than worse, performance.

We started by identifying circumstances in which we might expect an enhancement of the face inversion effect if our hypothesis is right. To explain how we went about this, we first offer a very brief resumé of our theoretical position, and then move on to consider the type of stimulus that might meet our requirements. These are a set of manipulated faces known as Thatcherised faces (face that have the eyes and the mouth rotated by 180 degrees, Thompson, 1980). In Experiment 1 we introduce these stimuli and offer some results that helped us to calibrate our later experiments. We used an *old/new recognition task* that showed normal and Thatcherised faces in upright and inverted orientations, and in addition to our main behavioural measure (accuracy used to extract d-prime sensitivity measure), we also recorded electrophysiological brain responses (EEG/ERPs) aiming to characterize the specific differences between the inversion effect for normal vs Thatcherised faces on the N170 ERP peak component.

The N170 peak component is a negative deflection maximal at 150-200 ms after the onset of a face stimulus at posterior temporal sites (Bentin, Allison, Puce, Perez, & McCarthy, 1996). Early studies suggested the N170 component as a neural signature of face “specificity” (Bentin et al., 1996; George, Evans, Fiori, Davidoff, & Renault, 1996) as it was found to be larger in amplitude and have a longer latency when responding to inverted compared to upright faces i.e. the inversion effect on the N170 (Eimer, 2000). However, in recent years a number of researchers, Rossion, Gauthier, Goffaux, Tarr and Crommelinck (2002) using Greebles (sets of mono-orientated novel objects), Busey and Vanderkolk (2005) using pictures of fingerprints and Civile et al (2014a, Experiment 4) using chequerboards drawn from a familiar (seen during the pre-exposure phase) prototype-defined category, have all provided evidence that the N170 peak component can be obtained and modulated (i.e. delayed and increased on inversion) for non-face categories of stimuli if they are made sufficiently familiar. Importantly, Civile et al (2014a) predicted and interpreted their results based on the same perceptual learning theory which is also the basis of the work done in Civile et al (2016a), Civile et al (2014a, b), and of the studies reported in the present paper. We will discuss that in detail in the next section.

In Experiment 2, we extended the tDCS procedure adopted in Civile et al (2016a), Civile et al (2018a) and Civile et al (2019) to the same behavioural paradigm (including the same stimuli) used in Experiment 1. The aim was to demonstrate how the combination of tDCS and Thatcherised faces can create circumstances (as mentioned earlier) where it could be possible to *enhance* the face inversion effect. Finally, in Experiment 3 we confirm the results obtained in Experiment 2 (i.e. that the tDCS procedure can enhance the face inversion effect). In addition, in Experiment 3, we provide, for the first time, a within-experiment demonstration (Experiment 3a vs 3b) of how our particular tDCS procedure can systematically enhance or reduce the inversion effect in different circumstances, allowing a comparison to be made between the two.

Theory

Here we explain our predictions based on the MKM model of perceptual learning (McLaren, Kaye and Mackintosh, 1989) using what has become known as the "differential latent inhibition of common elements" mechanism. This relies on modulation of the salience of a stimulus representation by means of error. If the elements (instantiated in the model as units) representing a stimulus are well predicted by other elements present (so that they have low error), then these elements will have a relatively low salience (unit activation). If, however, these elements are not well predicted, perhaps because they are novel, then their salience (activation) will be relatively high. This approach has been further developed and refined in McLaren and Mackintosh (2000) and McLaren, Forrest and McLaren (2012), but in essence the idea behind it is unchanged. It gives rise to perceptual learning for a discrimination between AX and BX when these stimuli are pre-exposed because the common, X elements are better predicted than the unique, A and B elements, and so have relatively low salience. It also predicts latent inhibition (in animals other than human, the analysis is more complex for humans) if a single stimulus, C is pre-exposed, because its' elements will become less salient. Hence the "differential latent inhibition" description of this mechanism given earlier.

The MKM theory, and its' instantiation as a model, depends on the modulation of salience by error to produce the perceptual learning that leads to the inversion effect seen in these experiments. The basic idea is very simple. As a result of experience with many faces, the elements representing features common to those faces, which will tend to be the prototypical ones, become strongly associated to one another (as well as having incoming associations from other features present in specific faces). This reduces their error scores, and the salience (in the model, activation) of the units representing those elements declines. Relatively novel, and hence unpredicted elements that tend to be specific to a given face do not have this reduction in salience. As a result, these "unique" features stand out, are more available for learning, and so improve discrimination between upright faces. This helps recognition, which also involves being able to tell faces apart. When faces are inverted, however, this learning based on previous experience no longer applies. We do not have great experience with inverted faces, and so they are not as easily discriminable as upright faces, and performance suffers. This analysis works for exemplars taken from any suitable prototype-defined category, hence the checkerboard result.

In order to generate a face inversion effect based on perceptual learning as a result of experience with faces, our analysis of the face inversion effect requires us to postulate a predominantly location specific coding of the features in a face, so that inverted faces will not (in general) benefit from perceptual learning. By this we mean that, to a first approximation, a given feature at a given location will activate different representational elements to those activated by the same feature at another location. This coding scheme is in line with that proposed in McLaren and Mackintosh (2002), and implementations of it are discussed in Livesey and McLaren (2011, 2019) and in Livesey, Pearson and McLaren, (2005). For present purposes, we can think of each feature in each location activating a number of representational elements, and some of these elements will be activated by combinations of features (again in specific locations). When a face is inverted, the features no longer occur in the same locations as was hitherto the case, and so a different pattern of activation of the elements results. On this basic account, an upright face and an inverted face are quite different stimuli that should be easily discriminable, which is clearly the case, but because of the relative novelty of the particular configuration of location-specific features found in unfamiliar inverted faces perceptual learning will be reduced. Evidence for the importance of location-specific feature information in discrimination learning comes from several sources (Oakeshott, 2002; Wills & Mackintosh, 1998).

Hence, the results obtained in Civile et al's (2016a) investigation of the checkerboard inversion effect, and the Civile et al (2018a) and Civile et al (2019) face inversion effect studies were interpreted as indicating that the tDCS procedure is changing error-based modulation of salience, so that instead of high error producing high salience, the effect is now the reverse. This may at first sight seem surprising. If we take it that tDCS reduces or abolishes the modulation of salience by error, then why would we argue that it is now predicted elements that would be more salient than unpredicted, novel elements in a stimulus? The answer is simply that the activation of an element/unit according to MKM is a function of how much input it receives. Salience modulation by error, when it is in operation, works by providing a boost to the input that an element receives that depends on its error. Now that this is no longer occurring, the input to an element is made up of the external input due to the feature corresponding to that element being perceived, and the internal input (i.e. the prediction) from other elements present. This latter, internal input will be greater for elements that are well predicted, and so they will be more active and hence more salient. In other words, by reducing or eliminating modulation of salience based on error, the system now reverts to its default, which is for low error units (because many other units are associated to them) to have a higher salience as a result of all the input that they receive from those other units. Thus, the well predicted elements are now the ones with relatively high salience or activation, and those that are not well predicted will have relatively low salience.

This explains why perceptual learning for stimuli drawn from a familiar category is abolished (checkerboards) or reduced (faces), because the common elements have now become the more salient ones, enhancing generalization and making it harder to discriminate between exemplars from the category. This effect does not apply to the inverted exemplars because of the relatively small amount of experience we have in seeing faces (or checkerboards from a familiar category) presented upside down, and so the difference in learning or performance between upright and inverted stimuli is reduced (resulting in a reduced inversion effect).

Thatcherised faces (Thompson, 1980; Bartlett & Searcy, 1993) are those where the mouth and eyes have been inverted within the face. There are a few subtly different procedures for doing this, for example the eyes can be rotated through 180° either as a unit, or individually as in Civile, McLaren and McLaren (2011), which is also the procedure we use here. The result is often a facial image that is perceived as rather striking (see Figure 1 for examples of our stimuli) when presented upright compared to when the same face is presented upside down. This effect is called the “Thatcher illusion”. Hence, in a Thatcherised face the mouth and eyes "stand out" and this gives an impression of a salient and unusual facial expression. We are able to provide an explanation for this illusion, based on the account of perceptual learning already given.

To see this, we need to apply the theory to Thatcherised faces, taking into account the fact that MKM asserts that the salience of a feature should be reduced when fully predicted, high when not predicted, and even higher when its opposite is predicted. We have already seen that inverted faces are treated as novel stimuli, which means that their features will all be equally salient, with no differential between common and unique features, making discrimination harder because learning to the common features results in generalization and they are at no disadvantage compared to the unique features. But what of the inverted features within a Thatcherised face? Here our analysis is somewhat different, and the crucial distinction is that, while in a novel stimulus or inverted face we assume that each representational element is not well predicted by the others present, in a Thatcherised face we assume that some of the predictions are systematically wrong. The result will be super-salient elements in the stimulus due to this enhanced error term, leading to learning to these features somewhat analogous to effects such as superconditioning. These elements will tend to dominate learning, as they will be more salient than both the "standard" common and the unique elements of that face. The exact nature of how this is done depends on the details of the coding scheme used to generate these representational elements, but we hope that this gives the general idea behind the assertion that Thatcherization will enhance the salience of some of the changed elements in a Thatcherised face. Using a similar argument to that deployed for normal faces, we assume that an inverted Thatcherised face will be treated, to a first approximation, as a novel stimulus. There is, of course, the difference that the eyes and mouth are, in some sense, in their correct orientation in an inverted Thatcherised face and this could have some impact on generalization, but they will be in the wrong location, and so we assume this to be something that, to a first approximation, we can discount.

Thus, we argue that a Thatcherised face would suffer from extra salience of the manipulated features (which gives the image such a striking impact on the viewer) due to the fact that elements of those features are now not just unpredicted, but incorrectly predicted. Many of these features will be common across Thatcherised faces, and this is what will give this class of stimuli its distinctive character, and also produces enhanced generalization between such faces resulting in reduced recognition performance. Inverted Thatcherised faces should not be subject to this problem to anything like the same extent, due the fact that we do not have enough experience in seeing inverted faces, so even if we rotate the eyes and the mouth the rest of the face would not be incorrectly predicting the eyes and the mouth to be in a specific orientation. Thus, Thatcherised faces should show a reduced inversion effect relative to normal faces, because of the reduced advantage for upright Thatcherised faces compared to inverted Thatcherised faces. Experiment 1 starts by investigating whether this is indeed the case with our procedures.

EXPERIMENT 1

Method

Subjects

We recruited 32 students (8 males; mean age = 19, age range = 18-22 years) from the University of Exeter. The experiment was approved by the research ethics committee at the University of Exeter. The sample size was based on Civile et al (2014a)'s study on the inversion effect for chequerboards on the N170. Hence, we used the same old/new recognition task, same number of trials (and structure), same EEG setup and data processing/analysis.

Materials

The study used 320 images of faces (http://pics.stir.ac.uk) of neutral expression (of non-famous individuals) in total, half female and half male. All faces were standardized using a grayscale color on a black background using Adobe Photoshop. For all faces we cropped the hair and the ears (we cropped the ears because in the female faces the ears were often covered by the hair). Both male and female faces were prepared in four different versions i.e. normal upright, normal inverted, Thatcherised upright and Thatcherised inverted. The Thatcherised faces were produced by rotating the mouth and each of the eyes individually by 180 degrees (Civile et al., 2011) (see Figure 1). The experiment was run using E-prime software Version 1.1 installed on a PC.

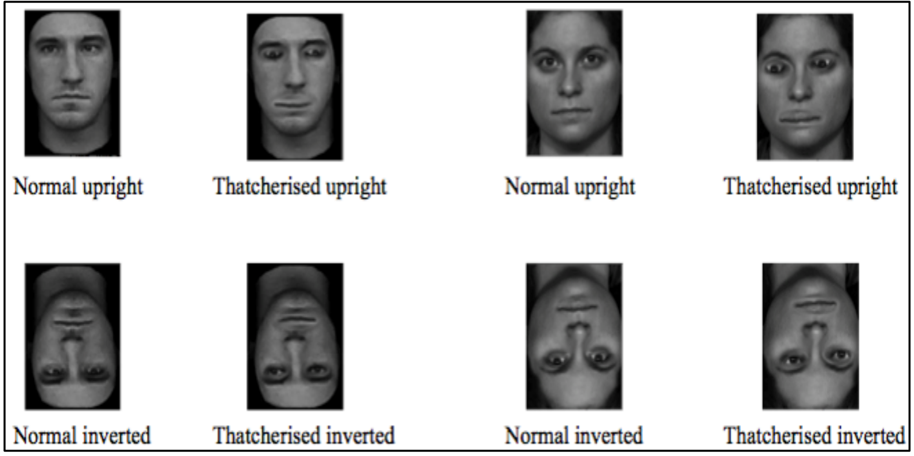

Figure 1. Examples of stimuli used in Experiment 1 showing the four different conditions for male (left) and female (right) faces (http://pics.stir.ac.uk). The stimuli, whose dimensions were 5.63 cm x 7.84 cm, were presented at resolution of 1280 x 960 pixels.

Procedure

The study used an *old/new recognition* task that consisted of two parts: a ‘study phase’ and an ‘old/new recognition phase’. To facilitate discussion of our results in relation to previous literature we adopted the same procedure and number of trials (and structure) as that used in Civile, Elchlepp, McLaren, Lavric and McLaren (2012) and in Civile, Elchlepp, McLaren, Galang, Lavric, and McLaren (2018b) studies on the inversion effect for the N170 with normal vs scrambled faces, and Civile et al.’s (2014a) study on the inversion effect in checkerboards that also looked at the N170. In the study phase, each participant was shown four different types of face (normal upright, normal inverted, Thatcherised upright and Thatcherised inverted) with 40 photos for each face type (half male and half female). In the test phase, another 160 novel stimuli of the same four types were added to this set. Each stimulus never appeared in more than one condition at a time during the experiment but served at some point in all conditions.

Trial Structure

After the instructions, the first part of the experiment involved subjects looking at 160 facial images presented one at a time in a random order. The subjects saw a fixation cross in the centre of the screen that was presented for 500 ms. This was followed by a blank screen for 500 ms and then by a facial stimulus that was presented for 3000 ms. Then the fixation cross and the blank screen were repeated, and another face presented until all stimuli had been seen. Following the study phase, after further instructions, there was an old/new recognition task in which subjects were shown (in random order) the faces they had already seen intermixed with a further 160 unseen faces split equally into the same face types as those already seen. During this *old/new recognition*, task each stimulus was presented for 4000 ms, subjects indicated whether or not they had seen the face onscreen during the study phase by pressing the '.' key if they recognized the face or by pressing 'x' if they did not (keys were counterbalanced). Four participant breaks were incorporated during this phase, allowing subjects to rest after they had viewed 80 faces.

EEG Apparatus

The EEG was sampled continuously during the study phase (across both old/new recognition tasks) at 500 Hz with a band-pass of 0.016-100 Hz, the reference at Cz and the ground at AFz using 64 Ag/AgCl active electrodes and BrainAmp amplifiers. There were 61 electrodes on the scalp in an extended 10-20 configuration and one on each earlobe. Their impedances were kept below 10 kΩ. The EEG was filtered offline with a 20 Hz low-pass filter (24 dB/oct) and re-referenced to the linked ears (Civile et al., 2012, Civile et al., 2018b; Civile et al., 2014a).

Behavioural Data Analysis

Our primary measure for all the behavioral results (Experiments 1, 2 and 3) presented in this paper was always performance accuracy in the old/new recognition task. The data from all the subjects in a given experimental condition was used to compute a *d'* sensitivity measure (Stanislaw & Todorov, 1999) for the recognition task (old and new stimuli for each stimulus type) where a *d'* of 0 indicates chance-level performance. To calculate *d'*, we used subjects' hit rate (proportion of YES trials to which the participant responded YES) and false alarm rate (proportion of NO trials to which the participant responded YES). Intuitively, the best performance would maximize H (and thus minimizes the Miss rate) and minimizes F (and thus maximizes the Correct Rejection rate); and thus the larger the difference between H and F, the better is the subject's sensitivity. The statistic *d'* ("d-prime") is a measure of 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 z-transforms of these 2 rates: $d' = z(H) - z(F)$ where neither H nor F can be 0 or 1 (if so, adjusted slightly up or down).

Each p-value reported in this paper is two-tailed, and we also report the F or t value along with measures of effect size (η^2_p). We also assessed performance against chance (*d'* of 0) to check that all face types in Experiment 1, 2 and 3 were recognized significantly above chance (for all conditions in the three experiments we found a $p < .01$). We analyzed the reaction times (RT) data to check for any speed-accuracy trade-off. We do not report these analyses here because they do not add anything to the interpretation of our results.

EEG Data Analysis

Peak amplitudes of the N170 in the study phase and recognition phase were examined for differences between the experimental conditions. N170 extraction was aided by linear decomposition of the EEG by means of Independent Component Analysis (ICA, Bell & Sejnowski, 1995). ICA was run separately for each subject using all scalp channels and the entire dataset. The remaining EEG segments were averaged for every participant and experimental condition. In each subject, we identified ICA components that: (1) showed a deflection (peak) in the N170 time-range (at 150-200 ms following stimulus onset), and (2) had a scalp distribution containing the 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 (mean 2.6; SD 1) - 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 (Civile et al., 2012; Civile et al., 2018b; Civile et al., 2014a). Three subjects had to be excluded because ICA did not find any components containing the N170 (nor was there an N170 visible in the original ERP). N170 latency and amplitude analyses were restricted to electrode PO8, (over the right temporal hemisphere) which often in the literature has shown bigger effects for the N170 (Civile et al., 2012; Civile et al., 2018b; Civile et al., 2014a; Rossion & Jacques, 2008). Furthermore, in agreement with Civile et al (2014a), Civile et al (2012) and Civile et al (2018b)'s studies, we found the ERPs effects to be stronger in the study phase. As previous studies have already suggested, this is not an unexpected result given that, if the modulation of the N170 reflects an effect of perceptual expertise, then this should occur when simply perceiving the stimulus and should be easiest to detect during the study phase, because the effect would not be confounded with having to do anything in particular, except perhaps attend to the stimulus, and by the recognition phase face processing might have been somewhat changed by experience of all the stimuli in the study phase. Thus, we report only the results from the study phase[1].

Results

Behavioural Results

A 2 x 2 within subjects ANOVA using as factors *Face Orientation* (upright, inverted) and *Face Type* (normal, Thatcherised) revealed a significant interaction between Face Type and Orientation $F(1, 31)= 7.75$, $p = .009$, $\eta^2_p = .20$. A significant main effect of *Face Orientation* was found (upright better), $F(1, 31)= 7.10$, $p = .012$, $\eta^2_p = .18$, as well as a significant main effect for *Face Type* (better performance on normal faces), $F(1, 31)= 33.20$, $p < .001$, $\eta^2_p = .51$. Follow up, paired *t* tests were conducted to compare performance on upright and inverted faces (the inversion effect) for each face type (normal, Thatcherised). We found a large inversion effect for normal faces, $t(31) = 5.36$, $p < .001$, $\eta^2_p = .48$, and a reduced, though still significant inversion effect for Thatcherised faces $t(31) = 2.42$, $p = .021$, $\eta^2_p = .16$. The significant interaction can thus be interpreted as being due to a reduced inversion effect in the Thatcherised faces.

Importantly, recognition performance for upright normal faces was significantly higher than that for Thatcherised faces, $t(31) = 3.55$, $p < .001$, $\eta^2_p = .29$. No significant difference was found between inverted normal and inverted Thatcherised faces, $t(31) = .157$, $p = .876$, $\eta^2_p < .01$ (see Figure 2).

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[1] In the Supplemental Material document we report the N170 Analysis for the test results from the old/new recognition task.

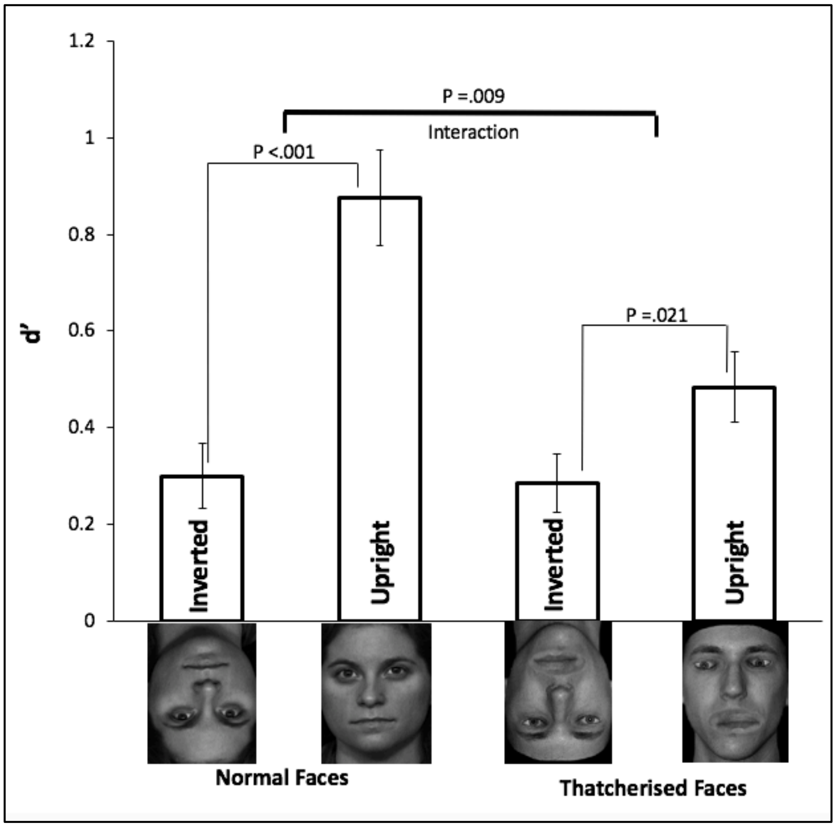

Figure 2. Behavioral results for the old/new recognition task in Experiment 1. The X-axis shows the four different stimuli' conditions, the Y-axis shows the mean *d'* for each condition. Error bars are SEM.

N170 Results

For the results on the N170 we conducted the same planned comparisons as for the behavioural data. As reported in detail below for both peak latencies and amplitudes we found very similar patterns of results to those found in the behavioural data.

Peak Latency. A 2 x 2 repeated measure ANOVA revealed a significant interaction between *Face Type* and *Orientation*, $F(1,28) = 4.73$, $p = .038$, $\eta^2_p = .14$. No significant main effect of *Orientation* was found, $F(1,28) = .164$, $p = .689$, $\eta^2_p < .01$. We found a significant main effect of *Face Type*, $F(1,28) = 12.33$, $p = .002$, $\eta^2_p = .30$. A simple effects analysis showed a significant inversion effect on the N170 for normal faces, with latencies to normal inverted faces (*M* = 174 ms, *SE* = 4.12) being significantly delayed compared to latencies for normal upright faces (*M* = 165 ms, *SE* = 4.11), *t*(28) = 4.60, *p* < .001, η^2_p = .43. This is our standard finding, but no significant difference was found between the latencies of Thatcherised upright (*M* = 168 ms, *SE* = 3.95) and Thatcherised inverted faces (*M* = 171 ms, *SE* = 3.87) faces, *t*(28) = 1.24, *p* = .224, η^2_p = .05. No significant difference was found between normal upright faces compared to Thatcherised upright faces (though there was a trend), *t*(28) = 1.80, *p* = .082, η^2_p = .10, nor between normal inverted faces and Thatcherised inverted faces *t*(28) = 1.38, *p* = .176, η^2_p = .06 (see Figure 3). For latencies, it would seem that the Thatcherised faces take intermediate values between those of upright and inverted normal faces. This corresponds quite straightforwardly to the pattern in the behavioral data.

Peak Amplitude. A 2 x 2 repeated measure ANOVA between *Face Type* and *Orientation* revealed a just significant interaction, *F*(1,28) = 4.18, *p* = .050, η^2_p = .13. No significant main effect of *Orientation* was found, *F*(1,28) = .912, *p* = .348, η^2_p = .03, nor of *Face Type*, *F*(1,28) = 1.71, *p* = .201, η^2_p = .05. A simple effects analysis showed a significant inversion effect for normal faces, with amplitudes for inverted normal faces (*M* = -.513μV, *SE* = 0.38) being larger (more negative) compared to amplitudes for upright normal faces (*M* = -.047μV, *SE* = 0.40), *t*(28) = 2.65, *p* = .013, η^2_p = .20. No effect of inversion was found for amplitudes in response to upright (*M* = -.451μV, *SE* = 0.40) and inverted (*M* = -.448μV, *SE* = 0.41) Thatcherised faces, *t*(28) = 0.01, *p* = .99, η^2_p < .01. The N170 peak for Thatcherised upright faces was marginally more negative than that for normal upright faces, *t*(28) = 1.95, *p* = .060, η^2_p = .12. No significant difference was found between inverted normal faces vs inverted Thatcherised ones, *t*(28) = .303,

$p = .764, \eta^2_p = .00$ (see Figure 3). In terms of amplitude, then, we can characterize our results as pointing to the upright normal faces differing from the three other face types.

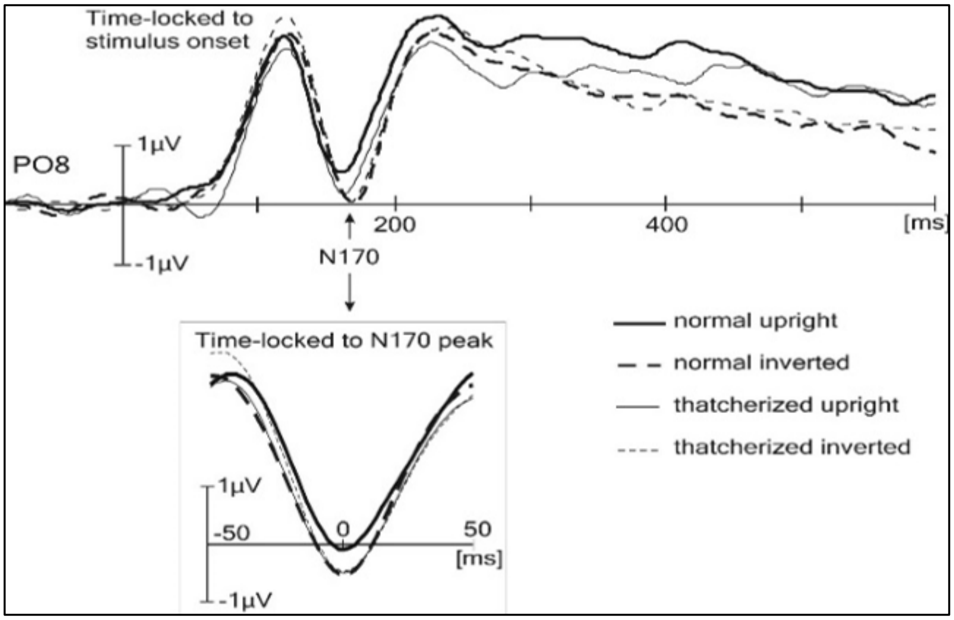

Figure 3. Waveforms at electrode P08 for the study phase. The X-axis shows the elapsed time after a stimulus was presented and the Y-axis shows the ERP amplitudes (µV). The insert in this figure shows the ERPs time-locked to the N170 peak (rather than the stimulus onset), for a clearer representation of ERP amplitude in the different conditions.

Additional Bayes Factor Analysis

Using the procedure outlined by Dienes (2011), we first conducted a Bayes analysis on the *Face Type* by *Orientation* interaction found in the behavioural results. Thus, we used the interaction found in Civile et al (2011, Experiment 1)'s study for normal vs Thatcherised faces (same stimuli as those used here) as the prior, setting the standard deviation of p (population value | theory) to the mean for the difference between the inversion effect for normal faces minus that for Thatcherised faces (0.56). We used the standard error (0.13) and mean difference (0.38) between the inversion effect for normal faces minus that for Thatcherised faces in Experiment 1 here. We assumed a one-tailed distribution for our theory and a mean of 0. This gave a Bayes factor of 26.03, which is very strong evidence indeed for the theory (because it is greater than 10, for the conventional cut-offs see Jeffrey et al., 1961), which in this case is that the interaction will be positive and non-zero.

Because in both Civile et al (2011, Experiment 1) and Experiment 1 here performance for normal upright faces was significantly better than that for Thatcherised upright faces, we calculated the Bayes factor for this effect using as a prior Civile et al (2011)'s Experiment 1, setting the standard deviation of p as the mean difference between normal upright faces minus Thatcherised upright faces (0.51). We then used the standard error (0.11) and mean difference (0.40) between normal upright faces minus Thatcherised upright faces in Experiment 1 of this paper. Once again, we assumed a one-tailed distribution for our theory and mean of 0. This gave a Bayes factor of 233.11, which is again very strong evidence that the performance for normal upright faces will be higher than that for Thatcherised upright faces in experiments of this type.

Discussion

Our results fit quite well with the accepted position on both the face inversion effect and the Thatcherisation manipulation. We have a strong face inversion effect, and a strong inversion effect on the N170 for normal faces in terms of both latency and amplitude. It's also worth noting that the performance on upright normal faces in this experiment is among the worst we have ever seen (mean d' less than 1), but this is in part due to the larger number of stimuli used in this experiment to ensure we had enough trial data for the ERP analysis. The effect of this would undoubtedly be to make the task quite a bit harder, but we suspect that there is more to it than that, and will have more to say about this later.

Performance on the Thatcherised faces was as expected, based on our own pilot data (Civile et al., 2011, Experiment 1) and on previous studies of this type (Bartlett & Searcy, 1993). We have a greatly reduced inversion effect (though still significant), which is mainly due to a reduction in performance on upright Thatcherised faces. The inverted faces were less affected by the Thatcherisation manipulation.

The results from the ERPs bolster this interpretation of the effects obtained as behavioral results. Running the same planned comparisons on the ERP data as for the behavioural data produces a very similar pattern of results, i.e. a strong inversion effect for the normal faces, a reduced effect for the Thatcherised faces, and a trend towards a significant difference in N170 amplitude between the upright normal and Thatcherised faces (p=.06) but not between the two face types when inverted.

In the past, there have been two studies similar to ours that have looked at the inversion effect for normal vs Thatcherised faces on the N170 peak amplitudes. Both studies showed a larger inversion effect (larger N170 peak amplitude for inverted faces compared to that for upright faces) for normal compared to Thatcherised faces (Milivojevic, Clapp, Johnson, & Corballis, 2003; Carbon, Schweinberger, Kauffmann, and Leder; 2005). Furthermore, Milivojevic et al (2003) using a gender decision task found an increased N170 peak amplitude for Thatcherised upright faces compared to normal upright faces. No differences were found between Thatcherised inverted and normal inverted faces. Carbon et al (2005) by adopting an identity decision task intended to test recognition of celebrities (Milivojevic et al. used images of non-famous people) also confirmed a larger N170 amplitude for Thatcherised upright faces compared to normal upright faces. However, the authors also found a smaller N170 amplitude for Thatcherised inverted vs normal inverted faces. Our results on the N170 peak amplitudes are broadly in line with both studies. Taking into account the particular images we used as our stimuli (we did not use photos of celebrities), our results would seem to be more comparable to those obtained by Milivojevic et al. (2003). Importantly, we also have the effects we found on the N170 peak latencies (the two other studies only investigated N170 peak amplitudes). Thus, both amplitudes and latencies' results show a larger inversion effect on the N170 for normal faces compared to Thatcherised faces.

Our results also fit in rather well with the effect on the N170 found by Roxane, Latinus, and Taylor (2006). The authors found a larger inversion effect on the N170 for normal faces compared to other objects (e.g. chairs, houses, cars) and animals (apes). More evidence in support of this finding comes from studies on the other-race effect and modulations of the N170 peak. Vizioli, Foreman, Rousselet, and Caladara (2010) showed that the N170 peak amplitude for inverted faces from an "own-race" set was significantly larger compared to that for upright own-race faces. And, this difference was reduced for faces taken from an unfamiliar ethnic grouping. Thus, the presentation of other-race faces seems to attenuate the effect of inversion on the N170 peak in a similar way to the manipulations we applied through Thatcherisation.

Overall, the results obtained from Experiment 1 were close enough to the predictions made on the basis of theory to encourage us to proceed with a tDCS experiment using Thatcherised and normal faces. The purpose of this next experiment is to investigate the effect that our tDCS procedure has in circumstances where we would argue that error-based salience modulation is actually making recognition harder (i.e. for the upright Thatcherised faces in Experiment 1) because it is emphasizing features that are common to a number of faces (e.g. all Thatcherised faces) and not unique to that particular face. We have already predicted that this would lead to stronger generalization between upright Thatcherised faces, causing the decrement in performance relative to normal faces just observed in Experiment 1. The rotated mouth and eyes in Thatcherised faces will have a high error, as they are incorrectly predicted, and will hence be relatively salient. These are the features that will be preferentially learned about during the study phase and will facilitate generalization of that learning. This will make performance to upright Thatcherised faces worse, and so reduce the inversion effect assuming that inverted Thatcherised faces are relatively unaffected (we have less experience in seeing faces presented upside down).

Given this, what can we expect from tDCS applied to Thatcherised faces? The answer follows from the analysis we have already offered. If the normal error-based modulation of salience is responsible for depressing performance on upright Thatcherised faces in this experiment, then reducing that effect by means of tDCS should improve performance on them. If, as expected, there is little impact on inverted Thatcherised faces, then the inversion effect should be enhanced, the opposite result to the one usually obtained with normal faces. This is our prediction for Experiment 2.

EXPERIMENT 2

Method

Subjects

Experiment 2 was run in two replications with 48 subjects each. The sample size was determined by earlier studies that used the same tDCS paradigm, same old/new recognition task, same face stimuli, and same counterbalancing (Civile et al.,2018a,b; Civile et al., 2016a). Analysis with replication as a factor showed that it did not interact significantly with any other factors in this experiment (max. $F[1, 92] = .320$, p = .57), nor does its inclusion as a factor materially change our analysis and so we collapsed over it. Hence, in total, 96 naïve (right-handed) subjects (32 male, 64 Female; Mean age = 20.4 years, age range= 18-25, *SD*= 1.94) took part in the study. Subjects were randomly assigned to either sham or anodal tDCS groups (48 in each group). All the subjects were students from the University of Exeter and were selected according to the tDCS safety screening criteria approved by the Research Ethics Committee at the University of Exeter.

Materials

Following Civile et al (2018b)'s study, we used 128 images of male faces selected from the set used in Experiment 1. As in Experiment 1, faces were shown in four different versions i.e. normal upright, normal inverted, Thatcherised upright and Thatcherised inverted. 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. Subjects sat about 70 cm away from the screen on which the images were presented.

The tDCS Paradigm

We used the same tDCS paradigm employed in Civile et al. (2016a), McLaren et al. (2016), Civile et al (2018a) and Civile et al (2019). The specific tDCS system was that used in Civile et al (2019). Hence, stimulation was delivered by a battery driven, constant current stimulator (Neuroelectrics) via a pair of surface sponge electrodes (35 cm^2), soaked in a saline solution and applied to the scalp at the target areas of stimulation. The study was conducted using a double-blind procedure reliant on the Neuroelectrics double-blind mode. We adopted a bilateral bipolar-non-balanced montage with one of the electrodes (anode/target) placed over the left PFC (Fp3) and the other was placed on the forehead, just above the right eyebrow (see Figure 4). 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 behavioural task and continuing throughout the study. In the sham group, subjects experienced the same 5 s fade-in and 5 s fade-out, but with the stimulation delivered for just 30 s in total.

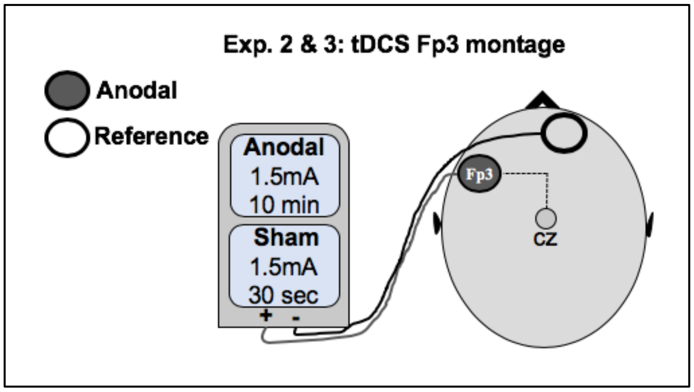

Figure 4. A schematic representation of the tDCS montage adopted in Experiment 2 and 3. This was the same montage used in Civile et al (2018a,b), McLaren et al. (2016) and Civile et al (2016a).

Procedure

As for Experiment 1, the *old/new recognition* task consisted of two parts: a ‘study phase’ and an ‘old/new recognition phase’ (Civile et al., 2019; Civile et al., 2018a ,b; Civile et al., 2016b; Civile et al, 2014b; Civile et al., 2011). In the study phase, each subject was shown normal and Thatcherised faces presented in the upright and inverted orientations (16 images for each type, 64 images in total). Faces were presented one at a time in random order. In the old/new recognition phase, 64 novel faces split into the same stimulus types were added to the 64 faces seen in the study phase, and all 128 images were presented one at a time in random order. Each face never appeared in more than one condition during the experiment for a given participant.

Trial Structure

Following the instructions, in each trial of the study phase subjects saw a fixation cross in the center of the screen presented for 1000 ms. After this, one of the faces was presented on screen for 3000 ms. The next trial started with the presentation of a fixation cross again. After all the 64 faces had been presented, the program displayed another set of instructions, explaining the recognition task. In this task, subjects were asked to press the '.' key if they recognized the stimulus as having been shown in the study phase on any given trial, or press 'x' if they did not (the keys were counterbalanced). During the recognition task, the faces were shown for 4000 ms during which time subjects had to respond.

Results

In reporting our results, we use standard ANOVA complemented, where appropriate, by planned comparisons based on our previous work and results. We computed a 2 x 2 x 2 mixed model ANOVA using, as within-subjects factors, *Face Orientation* (upright or inverted), *Face Type* (normal, Thatcherised) and the between-subjects factor *tDCS Stimulation* (sham or anodal). This revealed a significant main effect of *Face Orientation* $F(1, 94) = 68.26$, $p < .001$, $\eta^2_p = .42$, which is the usual inversion effect with better performance on upright than inverted faces. There was also a significant interaction between *Face Orientation* and *Face Type*, $F(1, 94) = 11.09$, $p = .001$, $\eta^2_p = .10$, which replicates the finding from Experiment 1 that the inversion effect is bigger in the normal than the Thatcherised faces. A significant main effect of *Face Type* was also found $F(1, 94) = 25.22$, $p < .001$, $\eta^2_p = .21$, which reflects the generally poorer performance with Thatcherised faces.

The interaction between *Face Orientation* and *tDCS Stimulation* was significant, $F(1, 94) = 7.32$, $p = .008$, $\eta^2_p = .07$, but there was no significant interaction between *Face Type* and *tDCS Stimulation*, or between *Face Orientation, Face Type* and *tDCS Stimulation*, max. $F(1, 94) =$

1.64, $p = .202$, $\eta^2_p = .01$. The effect of tDCS on the inversion effect in both types of face is the main novel result from this study. In part this is due to the expected result with the Thatcherised stimuli. The inversion effect in the sham group did not reach significance, $t(47) = 1.60$, $p = .115$, $\eta^2_p = .05$, whereas a significant inversion effect was found in the anodal group, $t(47) = 7.54$, $p = .008$, $\eta^2_p = .13$. The interaction between *Orientation* and *tDCS Stimulation*, however, was not significant, $F(1, 94) = .769$, $p = .38$, $\eta^2_p < .01$. The surprising aspect of these results is that a similar effect was observed in the normal faces. We found the usual significant inversion effect for normal faces in the sham group, $t(47) = 3.84$, $p < .001$, $\eta^2_p = .23$. But there was an enhanced inversion effect for normal faces in the anodal group $t(47) = 7.95$, $p < .001$, $\eta^2_p = .57$, in this case supported by a significant interaction between *Orientation* and *tDCS stimulation* for these faces, $F(1, 94) = 8.26$, $p = .005$, $\eta^2_p = .08$. We also directly compared the performance for upright faces in the sham vs anodal tDCS groups. This comparison is motivated by previous work where anodal tDCS delivered over the Fp3 was found to reduce performance for upright familiar checkerboards or faces, compared to the same condition in the sham group (Civile et al., 2018a; Civile et al., 2019; Civile et al., 2016a). This time, for the normal faces, our results show that anodal tDCS seems, if anything, to have improved performance for upright faces compared to sham, $t(47) = 1.75$, $p = .085$, $\eta^2_p = .05$. For the Thatcherised faces no significant difference (only a numerical trend) was found between upright faces in the anodal and sham groups, $t(47) = .042$, $p = .83$, $\eta^2_p < .01$ (see Figure 5).

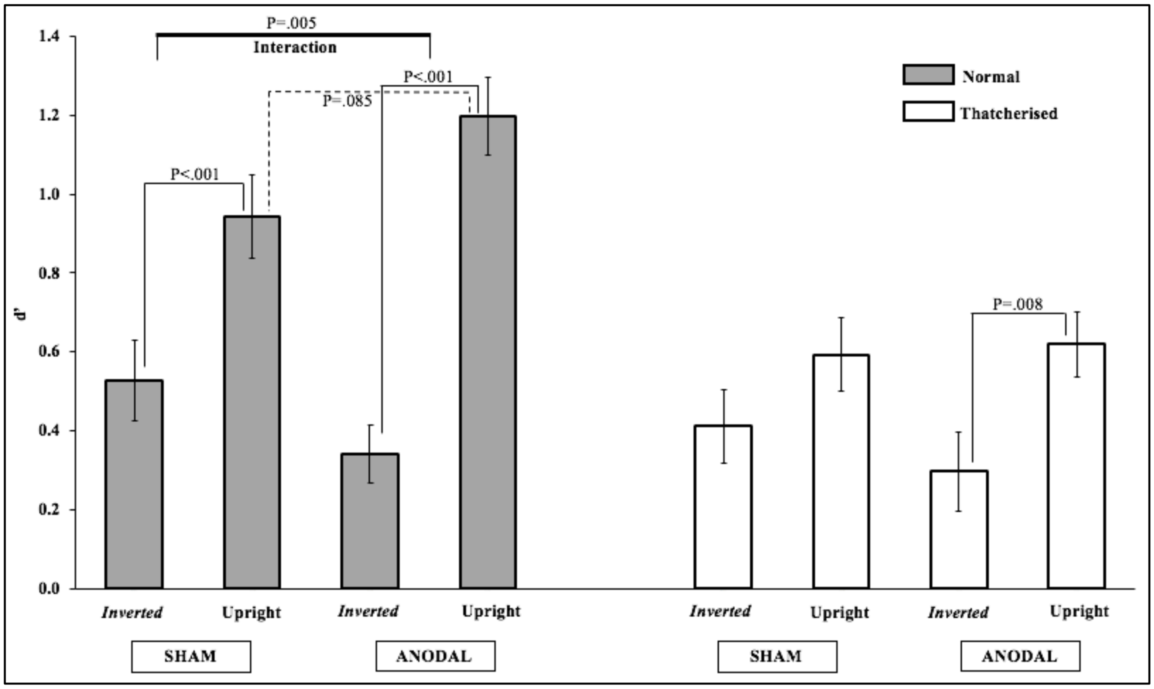

Figure 5. Results for Experiment 2. The *x*-axis shows the stimulus conditions for each tDCS group. The *y*-axis shows sensitivity d' measure (0 = 50% accuracy). Error bars represent s.e.m.

To further investigate the enhancement in the inversion effect for both face types induced by tDCS, we conducted an additional analysis using an inversion effect score obtained by subtracting the d' means for inverted faces (averaged across both Normal and Thatcherised faces) from those for upright faces in the sham and anodal conditions. A between-subjects comparison on this measure revealed a significant difference in support of the inversion effect in the anodal group being larger than that in the sham group, $t(47) = 7.66$, $p = .008$, $\eta^2_p = .14$.

Discussion

Previous studies (Civile et al., 2018; Civile et al., 2019) have demonstrated, that tDCS to normal faces in this type of experiment results in a reduced inversion effect with those faces, an effect in large part due to reducing performance on the upright faces. Now, by simply running the same type of experiment, using the same tDCS procedure but incorporating Thatcherised stimuli, we have obtained the opposite pattern of results. There is a significant enhancement of the face inversion effect in both normal and Thatcherised faces.

It is true that we expected the effect on Thatcherised faces, and indeed, this is why we ran the experiment. Our analysis was that error-based modulation of salience would be responsible for reducing performance to upright Thatcherised faces and so diminish the inversion effect, and that removing this via tDCS might actually enhance performance to these faces and so increase the inversion effect. This does seem to be the case, but we did not expect a similar effect on normal faces, in fact, quite the reverse. Our initial supposition was that performance on normal and Thatcherised faces would be relatively independent of one another because they are two fairly distinctive categories of face, and so any old / new decision making would be separated in some way for these two categories. Clearly, this supposition was incorrect.

But before we can accept this conclusion, and before we are justified in even attempting to provide an analysis of why we have obtained these results, we have to establish that these effects are real. That requires a replication of this result, but also an extension, to show that we can demonstrate, in a single experiment, both the reduction in the face inversion effect using tDCS (as previously showed by Civile et al., 2018a; Civile et al., 2019), and the enhancement that we have just found when running the same procedure in an experiment that has normal and Thatcherised faces mixed together. Experiment 3 does this.

EXPERIMENT 3

Method

The aim of Experiment 3 is straightforward: Within the same study we want to compare the effects of our tDCS procedure on the inversion effect when normal faces (male faces) are presented with other normal faces (in this case female faces that we have used for this purpose before), and contrast this with what happens when the same normal faces (male faces) are presented with Thatcherised faces (also male faces). Hence, on the one hand we aim to replicate the standard result showed in Civile et al (2018a) and Civile et al (2019), which is the reduction in the inversion effect after anodal tDCS. On the other hand, and within the same study, we want to confirm the *enhanced* inversion effect for normal faces and Thatcherised faces induced by the same anodal tDCS procedure. We predict this will occur if normal faces are presented with Thatcherised faces as in Experiment 2.

Subjects

Experiment 3 (3a & 3b) recruited 96 naïve (right-handed) subjects (26 male, 70 Female; Mean age = 20.3 years, age range= 18-23, *SD*= 0.95). Subjects were randomly assigned to participate in either Experiment 3a or 3b (48 in each experiment) and to either sham or anodal tDCS groups (24 in each group in each experiment). All the subjects were students from the University of Exeter and were selected according to the tDCS safety screening criteria approved by the Research Ethics Committee at the University of Exeter.

Materials

Experiment 3a used the same sets of male and female normal faces as those used in Experiment 1. Experiment 3b is a replication of Experiment 2 using the same normal and Thatcherised faces as were employed in that experiment.

The tDCS Paradigm

We used the same tDCS paradigm as that used in Experiment 2.

Procedure

For both Experiment 3a & 3b we used an *old/new recognition task* with the exact same number of stimuli and conditions as for Experiment 2. Experiment 3b was a direct replication of

Experiment 2, thus subjects were presented with male normal vs Thatcherised faces presented in both upright and inverted orientations. Experiment 3a presented the same male normal faces as for Experiment 3b but this time female normal faces replaced the male Thatcherised faces. Thus, male and female faces were presented in upright and inverted orientations. The two sub-experiments were conducted in parallel.

Results

The aim of the current study is to show how the tDCS procedure is able to systematically *reduce* and *enhance* the inversion effect. Thus, the primary analysis is the three-way interaction between the within-subjects factor *Orientation* (upright or inverted), and the between-subjects factors, *Experiment* (3a, 3b) and *tDCS Stimulation* (sham or anodal), which was found to be highly significant, $F(1,92) = 9.51$, $p = .003$, $\eta^2_p = .094$. As we shall see, this reflects the fact that we have produced the expected pattern of effects in both sub-experiments (see Figure 6). In Experiment 3a anodal stimulation decreases the inversion effect for both face types (normal male and female faces), whereas in Experiment 3b it has the opposite effect of increasing the inversion effect for both face types (Normal and Thatcherised male faces). This is also confirmed by the lack of a four-way interaction for *Orientation* (upright vs. Inverted) x *Face Type* (normal male faces vs. other, where other are female faces in Experiment 3a and Thatcherised faces in 3b) x *Experiment* (3a vs. 3b) x *tDCS Stimulation* (Anodal vs. Sham) which was not significant, $F(1,92) = .256$, $p = .60$, $\eta^2_p < .01$[2]. To further examine the effects induced by the tDCS procedure, we again calculated an inversion effect score by subtracting the d' means for inverted faces from upright faces for both the sham and anodal groups in each of Experiment 3a and 3b. In line with our previous studies (Civile et al., 2018; Civile et al., 2019), a between-subjects planned

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[2] In the Supplemental Material document we report another figure which shows the overall results broken down by condition and by sub-experiment for Experiment 3

comparison revealed a reduced inversion effect in the anodal group compared to the inversion effect in the sham group for Experiment 3a, $t(46) = 2.66$, p = .005 one-tail, $\eta^2_p = .24$. Critically, as predicted by the results of Experiment 2, the opposite pattern of results was found for Experiment 3b, where the inversion effect in the anodal group was larger than that found in the sham group, $t(46) = 1.81$, p = .038 one-tail, $\eta^2_p = .14$.

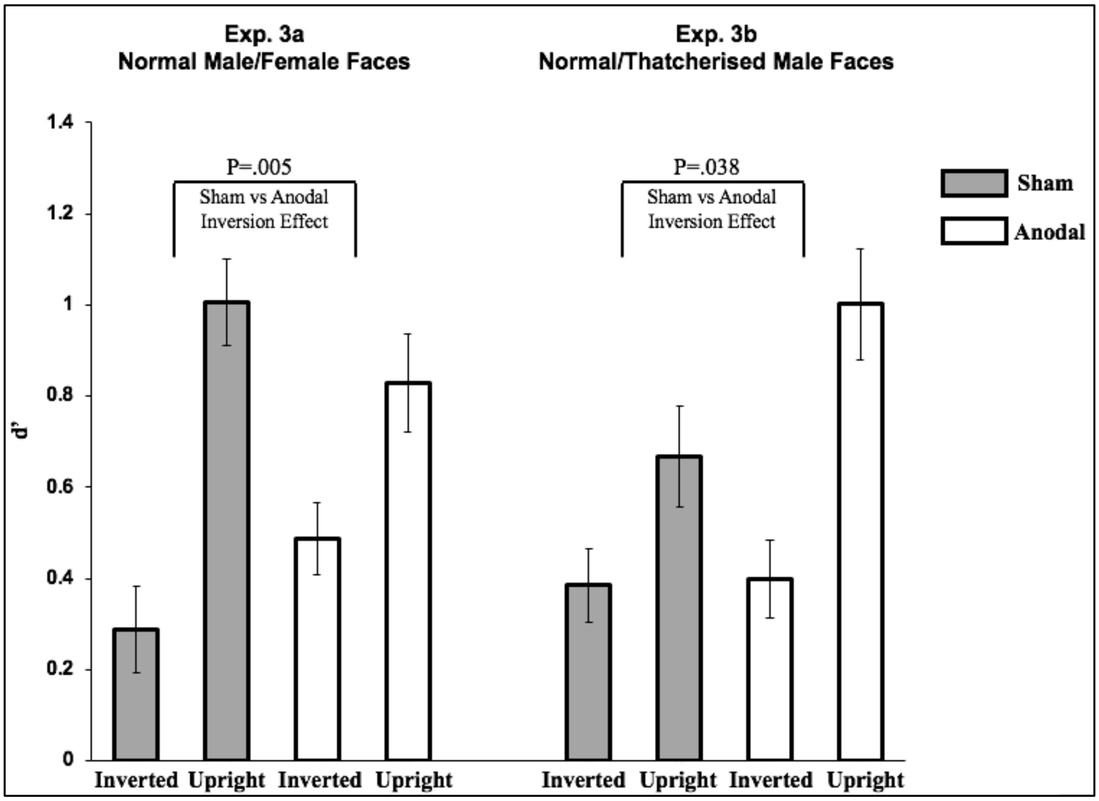

Figure 6. The results averaged over *Face Type* for each sub-experiment (Normal Male/Normal Female faces in Experiment 3a and Normal Male/Thatcherised Male Faces in Experiment 3b). The *x*-axis shows the stimulus orientation conditions for each tDCS group (sham in grey and anodal in white). The *y*-axis shows d'. Error bars represent s.e.m.

Turning now to the other three-way interactions, that between *Orientation* x *Face Type* x *tDCS Stimulation* was not significant, *F*(1,92) = .004, *p* = .95, η^2_p = .00, but the three-way interaction between *Orientation* x *Face Type* x *Experiment* approached significance, *F*(1,92) = 3.87, *p* = .052, η^2_p = .040. We can explain this by noting that, if we ignore the Stimulation factor, it is clear that the inversion effect for the "other" faces relative to the normal male faces differs between the two experiments. The inversion effect is smaller in the Thatcherised faces than that in the male faces in Experiment 3b. It is larger in the female faces in Experiment 3a, and rather similar to the inversion effect in the male faces in that experiment (as we would expect). In essence, then, this trend towards a significant interaction just reflects our standard finding that the inversion effect is diminished for Thatcherised faces and shows up as an interaction because of the design of our experiment. We should add that there is a main effect of *Face Type* as well, *F*(1,92) = 4.72, *p* = .032, η^2_p = .049, which also reflects the poorer performance to the Thatcherised faces. We also find a significant main effect or *Orientation*, *F*(1,92) = 73.48, *p* < .001, η^2_p = .44, which just confirms that upright faces were recognized better than inverted. All the other main effects and two-way interactions were not significant [with *Orientation* x *Face Type* being the closest to significance, *F*(1,92)= 1.32, *p* = .25, η^2_p = .01].

Additional Bayes Factor Analyses

We first conducted a Bayes analysis on the difference between the inversion effect score in the sham and in the anodal group in Experiment 3a. Thus, we used the same difference found in Civile et al (2018a)'s Experiments 1 & 2 averaged together as the prior, setting the standard deviation of p (population value | theory) to the mean for the difference between the inversion effect in sham group vs that in the anodal group (0.30). We used the standard error (0.09) and mean difference (0.38) between the inversion effect in the sham group vs that in the anodal group in Experiment 3a reported here. We assumed a one-tailed distribution for our theory and a mean of 0. This gave a Bayes factor of 2041, which is very strong evidence indeed that these results are what we would expect based on our previous work (Civile et al., 2018a, Civile et al., 2019).

Then we conducted a similar Bayes analysis on the difference between the inversion effect scores in the sham and in the anodal groups in Experiment 3b. We used the difference found in Experiment 2 as the prior, setting the standard deviation of p (population value | theory) to the mean for the difference between the inversion effect in the anodal group vs that in the sham group (0.29). We used the standard error (0.11) and mean difference (0.32) between the inversion effect in the anodal group vs that in the sham group in Experiment 3b here. We assumed a one-tailed distribution for our theory and a mean of 0. This gave a Bayes factor of 28.50, which is also very strong evidence that these results are what we would expect based on Experiment 2.

Discussion

The results of Experiment 3 fit very well with those of Experiments 1 and 2. Once again we have the weaker inversion effect in Thatcherised faces seen in Experiment 1. But more importantly, we have replicated the novel finding of an enhanced inversion effect in Thatcherised and normal faces when anodal tDCS is applied to Fp3 and both face types are tested together. At the same time, we have been able to replicate our standard reduction in the face inversion effect using these procedures when only normal faces are involved, and have also explicitly shown that these two effects differ significantly. It would appear that simply changing the other faces that are part of the study / test recognition paradigm completely changes the direction of effect obtained using our tDCS procedure, and our Bayesian analyses confirm this impression. In the discussion that follows, we attempt to explain why this should be so.

General Discussion

We begin by briefly reiterating our explanation for why the typical result using our tDCS procedure with normal faces is a reduction in the face inversion effect. We argue it is because our tDCS procedure affects the modulation of salience based on error that typically occurs when representing stimuli. One way of partially characterising this effect is to say that our neuro-stimulation procedure reduces the perceptual learning that would otherwise be exhibited for this class of stimuli in the orientation (upright) we would be more familiar with (i.e. it removes a certain kind of perceptual expertise), and this leads to poorer performance to these stimuli. As there is less of an effect on the stimuli in an unfamiliar (inverted) orientation, the net result is a diminution of the inversion effect.

When the tDCS procedure was used in Civile et al's (2016a) study with the checkerboard analogues of the face inversion effect, it completely abolished the inversion effect that we would otherwise expect with chequerboards taken from a familiar, prototype-defined category (McLaren & Civile, 2011; Civile et al., 2014a). The effect in these studies was based on stimulation during the period when people were familiarized with the chequerboard category, but the fact that Civile et al (2018a) and Civile et al (2019) also reduced the inversion effect obtained with normal faces using this procedure confirmed that it would work on stimuli for which expertise or perceptual learning had already been established. This was an important generalization of the result, but it is equally noteworthy that in no experiment have we succeeded (thus far) in completely abolishing the inversion effect with faces. We get a significant reduction in the inversion effect that leaves a still (typically highly) significant residual. This has led Civile et al (2018a) to speculate that this residual may be due to something other than expertise for faces, and may indeed reflect a "special" status for face processing. Whatever the explanation for this pattern of results, however, the reliability and replicability of that pattern has to be acknowledged.

The present experiments introduced Thatcherised faces into the mix because our analysis of them suggested that they might produce different results with our procedures. We argued that the manipulated features for these stimuli actually gain salience from error-based modulation, so that reducing or eliminating that modulation using tDCS should reduce this effect, and hence change performance to these faces. On the assumption that these features will tend to be ones that generalize across Thatcherised faces (giving them their distinctive quality that allows them to be classified as "Thatcherised stimuli"), the prediction was that performance on upright Thatcherised faces should improve with tDCS, and hence the inversion effect for these faces should be enhanced. Broadly speaking, we have confirmed that prediction. In Experiment 2 the inversion effect in the Sham group is smaller in Thatcherised faces, and performance to those faces is generally worse than to normal faces (as was also the case in Experiment 1), but we do have evidence that tDCS enhanced the inversion effect for Thatcherised faces. This pattern of results is replicated in Experiment 3. In both experiments, the response to neuro-stimulation for Thatcherised faces was the same as that for the accompanying normal male faces, and we have reported the relevant interactions in our results sections. Our claim that tDCS enhanced the inversion effect in these faces rests on the overall *Orientation* by *tDCS Stimulation* interaction, and the lack of any interaction of this effect with Face Type.

The question that now needs to be addressed is why the inversion effect for normal male faces is also enhanced in these experiments. To understand our tentative explanation of this effect, we first need to reframe our explanation of the basic perceptual learning effect in the Sham conditions that we argue produces better performance to the upright faces than would otherwise be the case, thus promoting an inversion effect for these stimuli. Why do we get better performance for these upright stimuli? What do we mean by "perceptual learning" here? Put simply, we mean that modulation of salience on the basis of error is enhancing the salience of the representational features (elements) that are distinctive to a particular exemplar (i.e. a particular face) relative to those that are common across faces. By doing this, it reduces the generalization from a face that is studied to other, non-studied faces. This then helps discriminate “old” from “new” faces during the recognition phase. In other words, the result of perceptual learning here is reduced generalization. When tDCS is applied to these faces, we expect them to lose this advantage, and so performance on upright faces would drop, performance on inverted faces would be largely unaffected, and hence the inversion effect would be reduced (Civile et al., 2018a, Civile et al., 2019).

But this analysis assumes that there is no generalization between Thatcherised and normal faces, that they are, in some sense, independent of one another. This is the assumption that, in retrospect, we can now see is very hard to justify. First of all, the stimuli are all still faces, so of course there will be generalization between them, but that is by no means enough to explain the observed enhancement. There is generalization amongst normal faces themselves, but we still get a diminution in the inversion effect with our tDCS procedure applied to such faces as those used in Experiment 3. But whilst it is quite reasonable to assume that some of the changed, and hence highly salient features in a Thatcherised face will be common across that class of faces and not generally found in normal faces, there is no reason why all these features should fit this specification. It is quite possible that there will be some salient features that generalize to normal faces. This would make discrimination of seen from unseen normal faces harder. And equally, we should not forget there will be unchanged features (e.g. the nose) in a Thatcherised face that are common to many faces. These will, of necessity, become more salient as a result of Thatcherisation, because many of the features predicting them (and lowering their error) have themselves changed. This will have an impact in promoting generalization from seen Thatcherised faces to both seen (where we assume it will have little effect) and unseen normal faces, making discrimination between them on test that much harder.

In fact, we did think of these considerations at the outset, but simply assumed that any such effects would be less important than the reduced generalization obtained via standard perceptual learning for upright normal faces. The data from Experiments 2 and 3 now compel us to revise this assumption. If we instead assume that generalization from upright Thatcherised faces to upright normal faces in these experiments is sufficient to substantially affect performance on the latter, then we can explain the effect of tDCS on these faces. If generalization from Thatcherised faces to normal faces is making performance on the normal faces worse than it otherwise would be, and if this generalization is dependent on error-based modulation of salience, then applying tDCS that changes that modulation will release the upright normal faces from this effect and performance will improve, just as we have observed in Experiments 2 and 3.

The basic idea behind our explanation is that generalization from upright Thatcherised faces is driving down performance on upright normal faces in the sham condition, reducing the inversion effect there, and that tDCS releases the upright normal faces from this effect and so enhances the inversion effect. There are some quite strong corollaries to this explanation of our results that we will now outline. One is that our explanation cannot work unless there is a component of the face inversion effect that is not attributable to perceptual learning based on modulation of salience via error. We have already noted that this is one possible reason for why we have never been able to abolish the inversion effect in faces using tDCS, but now we have to subscribe to it completely. Put simply, the explanation of our results hinges on the extra generalization between face types that is due to error-based modulation of salience making performance on upright faces worse than it otherwise would be, driving down the inversion effect rather than enhancing it. This can only work if there is an inversion effect to drive down that does not rely on this salience modulation. The perceptual learning that would typically be the consequence of this salience modulation mechanism for the normal faces, and that would normally contribute to the inversion effect, must already be more than compensated for by this enhanced generalization between the two face types.

Realising this quite naturally leads to the conclusion that the inversion effect in our normal faces that are accompanied by Thatcherised faces in the Sham condition of Experiment 3b should be less than that exhibited by the same faces when accompanied by female faces in the Sham condition of Experiment 3a. And numerically this is the case (see Figure 7 in the Supplemental Material file), though the effect is not significant. It is also worth reiterating that the inversion effect we see in normal faces when tested in combination with Thatcherised faces is rather lower than we are used to, as is the case for Experiment 1 of this paper (again see Figure 7 in the Supplemental Material file). But we would caution the reader in interpreting these results. There are more factors than salience and its modulation by error influencing generalization here. Another factor that is important is the similarity between the two types of face involved in the experiment. To see this, first imagine that instead of either Experiment 3a or 3b, we ran an experiment just like them where all the faces were normal male faces. What might we expect? Having so many faces drawn from the same category will make discrimination difficult and performance might be poor as a consequence. Now contrast this with running another experiment where the other "type" of face is in fact a checkerboard category. Now we would not expect anything like so much difficulty in discriminating between seen and unseen faces, because the checkerboards really would be that independent class of stimuli we had assumed in our earlier analysis. Clearly, female faces are much more like accompanying male faces than checkerboards, and so the task in Experiment 3a is more akin to our difficult example. Given this, the lack of a significant difference between the inversion effect for normal male faces in the Sham conditions of Experiments 3a and 3b is perhaps not so surprising. If we were to compare 3b with our hypothetical faces and checkerboard experiment then we might expect to get a clearer result, and this will ultimately be the correct way to test this hypothesis.

There is a way of thinking about the inversion effect and its components that can at first sight cause problems for the analysis that we have just given. It begins by noting that the normal inversion effect for faces is made up of two components, one not dependent on perceptual learning of the type under consideration here (A), and the other that is generated by it (B). Our tDCS procedure usually eliminates this second component, thus reducing the inversion effect (i.e. leaving only A). Now, if the assumption is that in Experiment 3a this analysis holds, and the inversion effect is made up of these two components (A+B), and in 3b the salience modulation component that enhances the effect in 3a is instead reducing it giving A-B, then the only possible effect of tDCS is to bring the two groups both closer to a value of A by getting rid of the B component. Thus, the difference in inversion effect for normal faces between the Anodal groups in Experiment 3 should be small, and the difference between the Sham groups should be large. This is quite clearly not the case, but that is because the analysis is flawed.

The problem with the analysis is that it once again ignores the other factors that determine the difficulty of the task. In other words, the size of the inversion effect in Experiment 3a and 3b, after any component due to perceptual learning is factored out, will not necessarily be the same because the tasks themselves can still differ in difficulty. The set of faces involved in 3a will actually make recognition harder (because the to-be-remembered items are more similar) than the set used in 3b, and that will influence performance to normal upright faces. Thus, whilst we can speak of components A and B for any inversion effect, that does not mean that the size of the effect due to A will be the same in each sub-experiment. In fact, once salience modulation by error is removed from the equation, then Thatcherised faces will be less similar to normal faces and will generalize less to them than female faces. Exactly how the effects due to stimulus similarity influencing task difficulty and salience modulation balance out is a parametric matter, making the relative strength of the inversion effect in the Sham conditions in Experiment 3 a matter for empirical analysis. But we can be sure of one thing, wherever we start from in the Sham conditions, the Anodal tDCS conditions should have opposite effects in 3a and 3b. Hence the interaction is the one effect that we can state should be present *at priori*, and it is.

The analysis we have just given may seem rather speculative and post-hoc. But the point here is that something is needed to explain these results, and the analysis offered does have the merits of being consistent with our previous results and position on perceptual learning, and it gives a theoretically motivated explanation of the results reported in this paper. Certainly, the level of generalization from Thatcherised to normal faces that we have to postulate is surprising (it surprised us), but the result is itself surprising and makes the case for the need for new assumptions. As we have already said, the real test of this proposition will be in investigating the effect of combining normal and Thatcherised faces in recognition studies and comparing this to situations where the normal faces are combined with some other class of stimuli that should not generalize to them.

We have given a very detailed and molecular analysis of generalization influenced by salience modulation and stimulus similarity as applied to the faces used in these experiments. But this focus on detail, both in terms of theory and experimental results should not blind us to the bigger picture. This is that we have found a set of circumstances where tDCS reliably enhances the inversion effect. Demonstrating that our tDCS procedure can improve performance is, we believe, the main finding here. It at once rules out various already quite unlikely accounts of what tDCS is doing based on it simply making performance worse. Now that we know that it does not always make performance worse, but in the right circumstances has the opposite effect, we no longer need to be concerned with those possibilities. Instead, we have a reliable pattern of data that fits (with some additional assumptions) with our model of perceptual learning and promises to open the path to applications where changing the way that people process stimuli would be of real benefit.

Our results contribute to a recent line of research that investigates the effect of tDCS on perceptual learning and/or face processing, though these studies tend to differ in detail from our procedures. Pisoni, Vernice, Iasevoli, Cattaneo and Papagno (2015) studied the effects of anodal tDCS (compared to sham) on an unfamiliar face-name association learning task. Name retrieval was tested by asking the participants to recall the name of a face image they had just been presented with and by selecting the correct name associated to a face image given two alternatives. The authors found that when anodal tDCS was delivered over the left ATL (Anterior Temporal Lobe) at T3 location (determined by the 10-20 EEG electrode positioning) performance was disrupted compared to sham (Pisone et al., 2015, Experiment 1). In another study, Peters, Thompson, Merabet, Wu, and Shams (2013) applied anodal tDCS over the primary visual cortex (V1, corresponding to Oz on EEG channel positioning) when participants performed a contrast detection task on two consecutive days. The specific task engaged participants in a two-alternative forced choice in which they had to indicate the orientation (horizontal or vertical) of the stimuli presented (Gabor patches). On day 1 a group of participants received anodal stimulation, whereas another group received cathodal stimulation. The stimulation polarity was then reversed on day 2. A third group of participants received sham stimulation on both days. Interestingly, task performance improvement was recorded between day 1 and day 2 for the participants who received cathodal stimulation on the day 1 and those who received sham. No improvement was found for participants who were administered anodal stimulation on day 1. The authors suggested that anodal tDCS blocked overnight consolidation of perceptual learning.

Despite there not being many studies (in addition to Civile et al., 2018a, Civile et al., 2019 and the current paper) that have tested the effects of tDCS directly on face recognition, Yang et al (2014) and Barbieri, Negrini, Nitsche, and Rivolta (2016) have provided some evidence of how anodal tDCS applied over occipital sites could lead to an improvement in performance. Yang et al (2014, Experiment 2), showed that anodal tDCS led to a reduced composite face effect (impairment at recognizing the top half of a familiar face when matched with the bottom half of another familiar face) by enhancing performance for incongruent faces (composite faces created by mismatched top and bottom halves). In a similar vein, Barbieri et al (2016) found that anodal tDCS delivered on the P08 channel area enhanced memory performance for both upright faces and objects (inversion was not tested) compared to sham. Where we differ from these studies is in both the nature of the stimulation applied, and in the theoretical analysis of why that stimulation produces the results it does. Nevertheless, taken together, our results and those from the studies reviewed here all contribute to an emerging line of research that suggests that the use of advanced neuro-stimulation techniques can help us to modulate and, in some circumstances, enhance perceptual learning and face recognition skills. We look forward to pursuing this further in the future.

Acknowledgments

This project has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Curie grant agreement No.743702 awarded to Ciro Civile; and 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).

We would like to thank the undergraduate students S. Whittingham, C. Ransom, C. Tam Ching and S. Minami, for their help in running some of the participants recruited for Experiments 2 & 3.

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SUPPLEMENTAL MATERIAL

EXPERIMENT 1

N170 Results: Old/New Recognition task

Peak Latency. In the recognition phase the 2 x 2 repeated measure ANOVA revealed no significant interaction between *Face Type* and *Orientation*, $F(1,28) = .117$, p = .667. A simple effect analysis showed a significant inversion effect on latencies to inverted normal faces (M = 168 ms, SE = 3.76) which were significantly delayed compared to latencies for upright normal faces (M = 162 ms, SE = 3.97), $t(28) = 4.045$, SE = 1.29, $p < .001$, $\eta^2_p = .36$. A significant inversion effect was also found between upright (M = 165 ms, SE = 4.61) and inverted (M = 169 ms, SE = 3.79) Thatcherised faces, $t(28) = 2.574$, SE = 1.60, $p = .016$, $\eta^2_p = .19$. No significant difference was found between normal upright faces vs Thatcherised upright faces $t(28) = 1.507$, $p = .143$ (see Figure attached below).

Peak Amplitude. A 2 x 2 repeated measure ANOVA revealed no significant interaction, $F(1,23) = .009$, p = .925. A planned comparison showed a not significant inversion effect for inverted normal faces (M = -.728μV, SE = 0.37) amplitudes compared to upright normal faces (M = -.385μV, SE = 0.41), $t(28) = 1.584$, $p = .11$. A not significant effect of inversion was recorded for the amplitudes corresponding response to Thatcherised upright (M = -.542μV, SE = 0.40) vs inverted (M = -.907μV, SE = 0.45) faces, $t(28) = 2.144$, SE = .170, $p = .38$, $\eta^2_p = .14$. No significant difference was found between normal upright faces vs Thatcherised upright faces $t(28) = .958$, $p = .346$ (see Figure S1).

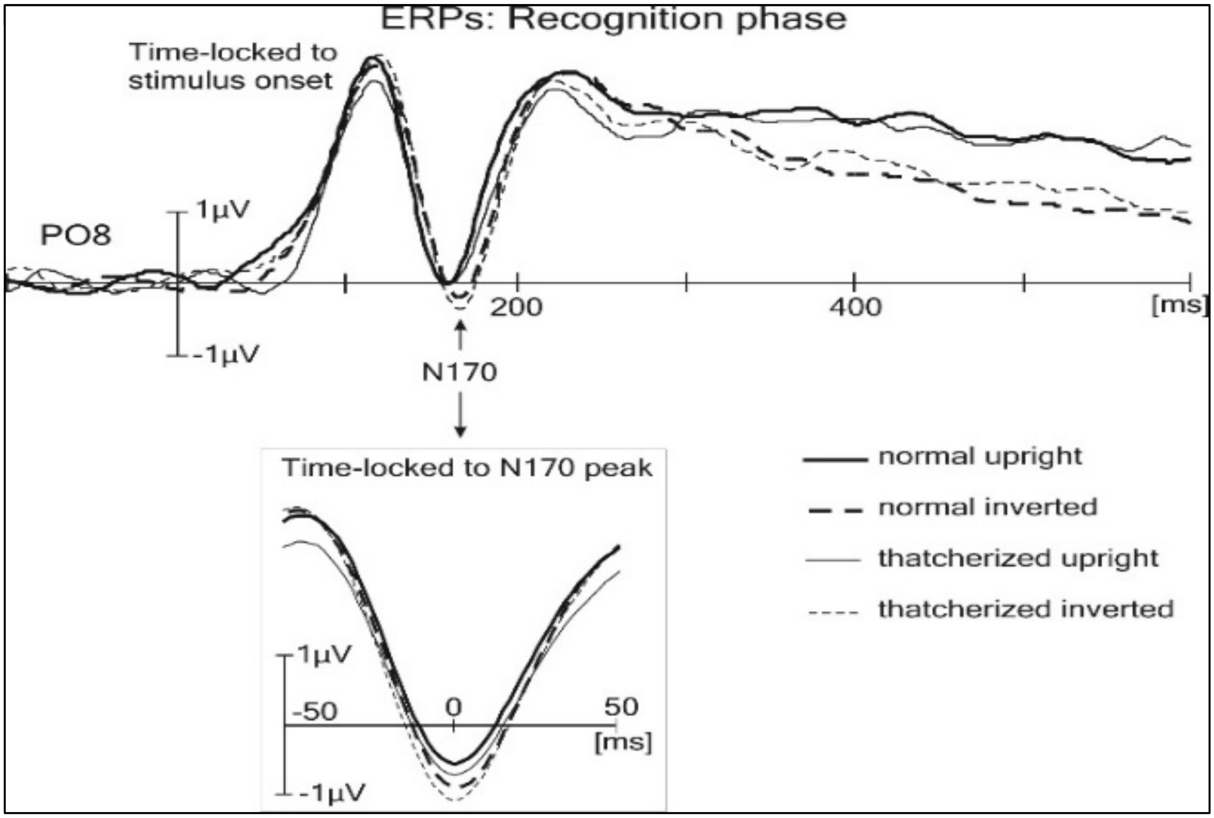

Figure S1. Waveforms at electrode P08 for the recognition task. The X-axis shows the elapsed time after a stimulus was presented and the Y-axis shows the ERP amplitudes (µV). The insert in this figure shows the ERPs time-locked to the N170 peak (rather than the stimulus onset), for a clearer representation of ERP amplitude in the different conditions.

EXPERIMENT 3

Experiment 3a and 3b overall results Figure

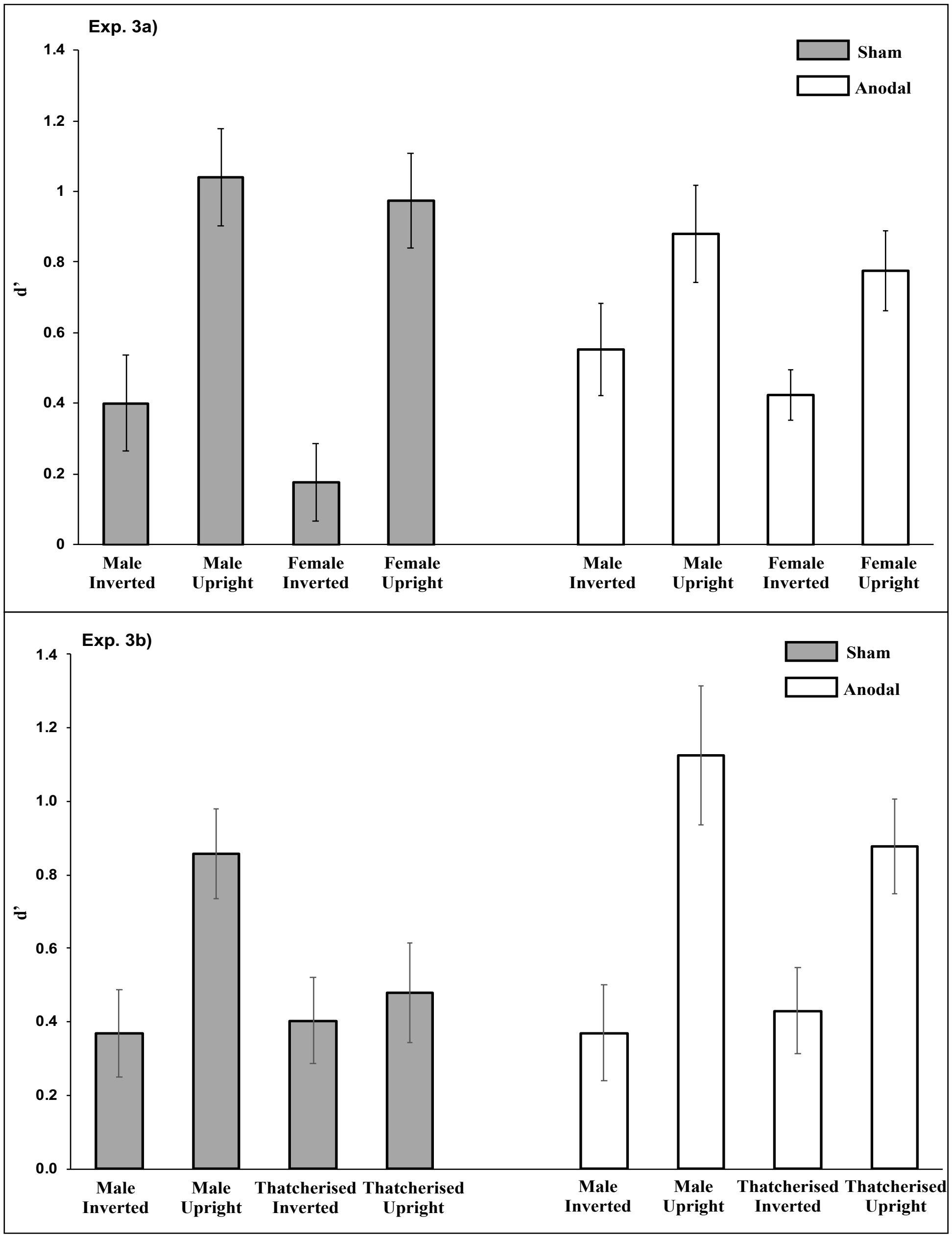

Figure S2. The results broken down by condition and by sub-experiment for Experiment 3. Top panel Experiment 3a, bottom panel Experiment 3b. Sham conditions are on the left of each figure. The *x*-axis shows the stimulus conditions for each tDCS group. The *y*-axis shows sensitivity d' measure (0 = 50% accuracy). Error bars represent s.e.m.