



The role of experience-based perceptual learning in the face inversion effect

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ABSTRACT

Perceptual learning of the type we consider here is a consequence of experience with a class of stimuli. It amounts to an enhanced ability to discriminate between stimuli. We argue that it contributes to the ability to distinguish between faces and recognize individuals, and in particular contributes to the face inversion effect (better recognition performance for upright vs inverted faces). Previously, we have shown that experience with a prototype defined category of checkerboards leads to perceptual learning, that this produces an inversion effect, and that this effect can be disrupted by Anodal tDCS to Fp3 during pre-exposure. If we can demonstrate that the same tDCS manipulation also disrupts the inversion effect for faces, then this will strengthen the claim that perceptual learning contributes to that effect. The important question, then, is whether this tDCS procedure would significantly reduce the inversion effect for faces; stimuli that we have lifelong expertise with and for which perceptual learning has already occurred. Consequently, in the experiment reported here we investigated the effects of anodal tDCS at Fp3 during an *old/new recognition* task for upright and inverted faces. Our results show that stimulation significantly reduced the face inversion effect compared to controls. The effect was one of reducing recognition performance for upright faces. This result is the first to show that tDCS affects perceptual learning that has already occurred, disrupting individuals' ability to recognize upright faces. It provides further support for our account of perceptual learning and its role as a key factor in face recognition.

1. Introduction

Perceptual learning refers to an enhanced ability to distinguish between similar stimuli as a consequence of experience with them or stimuli like them, and plays a key role in learning to identify stimuli as specific exemplars of a category, and not confuse one stimulus with another, similar one (e.g. wine experts and wines, or bird watchers and warblers; James, 1890; see Hall, 1980 for a review). We know that people (and other animals) can improve their perceptual skills as a result of experience with stimuli, and recent studies have shown this phenomenon to be responsible for some key perceptual skills that people possess, in particular, that it contributes to their ability to distinguish between faces and recognize individuals. For example, if we pre-expose someone to a set of checkerboards, all of which are produced by imposing random variation on one original prototype checkerboard, then this will have the effect of making them better able to distinguish between exemplars generated in this way – a basic perceptual learning effect. They will now be able to tell two otherwise similar checkerboards apart where once they might have found it difficult to do so, and such *pre-exposure* improves their ability to identify checkerboards they have been asked to memorize in a subsequent

recognition test (McLaren, Leevers, & Mackintosh, 1994). McLaren (1997) extended this result to show that the same procedures could also produce an inversion effect, with upright exemplars discriminated better than inverted ones.

Civile, Zhao, et al. (2014) further developed the case for perceptual learning as a contributor to the *face inversion effect* (i.e. that upright faces are recognized much better than inverted ones), by showing that these results can be obtained with the kind of *old/new recognition* paradigm conventionally used in such studies (Diamond & Carey, 1986; Yin, 1969; see Maurer, Le Grand, & Mondloch, 2002 for a review). Participants were trained to categorize (categorization task) checkerboard exemplars from two prototype-defined categories (the pre-exposure phase), before being shown an equal number of checkerboard exemplars (which they had not previously encountered) drawn from either one of the now familiar categories or a novel category, half of which were upright and half inverted. Participants were then tested for recognition of these exemplars after this study phase. The results confirmed the inversion effect for checkerboard exemplars drawn from a familiar category, and its absence for exemplars drawn from a novel category, strengthening the case for perceptual learning contributing to the inversion effect found with faces.

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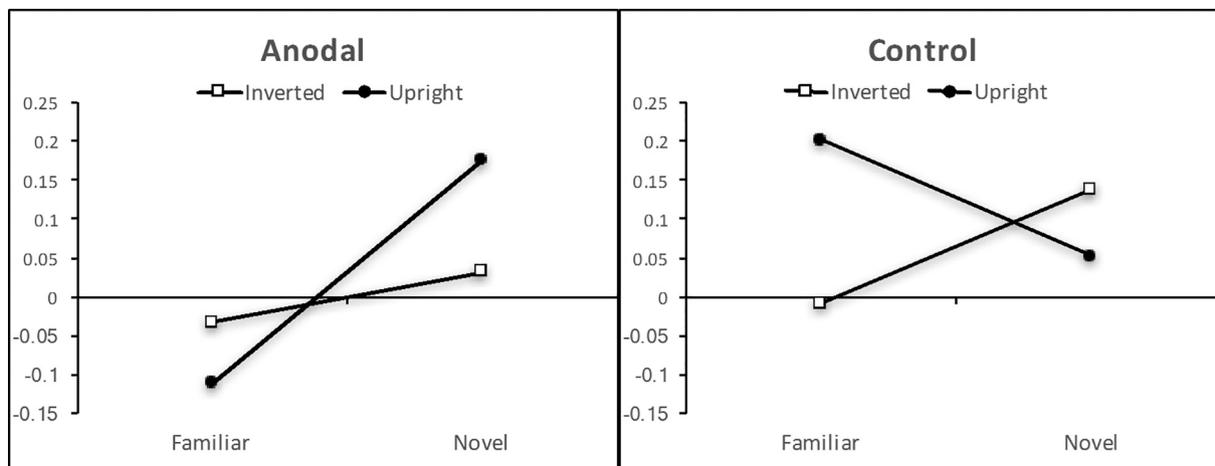


Fig. 1. This shows the combined results of the studies reported in Civile et al. (2016) broken down by stimulation type (Anodal or Control). The y-axis shows the mean d' score for the recognition test on the checkerboards at the end of the experiment. Familiar refers to checkerboard exemplars that were drawn from a familiar (i.e. pre-exposed) category. Novel denotes that the category, and hence exemplars, had not been pre-exposed to that participant. Filled circles show data points for upright stimuli (i.e. in the same orientation as during pre-exposure), open squares inverted stimuli that have been rotated by 180° . This is a dummy variable for the Novel category stimuli.

In a recent study, Civile, Verbruggen, et al. (2016) demonstrated that tDCS over Fp3 significantly affected perceptual learning and reduced the inversion effect that can otherwise be obtained with checkerboards (see Fig. 1). The authors adopted the same old/new recognition task as in Civile, Zhao, et al. (2014)'s study which uses a categorization task to pre-expose participants to the stimuli i.e. checkerboards. Hence, the authors employed the same tDCS montage previously used in other categorization experiments (e.g. Ambrus et al., 2011) delivering tDCS stimulation at 1.5 mA to the Fp3 site when participants were performing the categorization task. Civile, Verbruggen, et al. (2016) showed that the control condition (sham tDCS stimulation over Fp3 delivered during the *pre-exposure* phase, i.e. the checkerboard categorization task, see right panel of Fig. 1) replicated the usual inversion effect (see Civile, Zhao, et al., 2014 for multiple demonstrations of this effect) for checkerboards drawn from the Familiar category (difference between solid circle and open square), but, as expected, not for checkerboard exemplars drawn from a Novel category that had not been pre-exposed. Critically, anodal tDCS to the same brain region changed this pattern (left panel of Fig. 1), as there was now no significant inversion effect for stimuli drawn from the Familiar or Novel categories, and upright exemplars drawn from a familiar category were less well recognized than those drawn from the novel category (difference between solid circles), an indication that perceptual learning may even have been reversed. This remarkable and informative result suggested that perceptual learning in humans could be turned 'on' and 'off'

Civile, Verbruggen, et al.'s (2016) study is the first evidence that anodal tDCS administered during the pre-exposure phase can affect perceptual learning later on when participants are asked to memorize and recognize exemplars of checkerboards drawn from the checkerboard categories seen in during the pre-exposure phase (categorization task). The next important question to address is whether or not the same tDCS procedure would also affect perceptual learning that has already taken place. Given the lifelong expertise we have for faces, and given the already established analogy between the inversion effect obtained with checkerboards (Civile, Zhao, et al., 2014; Civile, Verbruggen, et al., 2016; McLaren, 1997; McLaren & Civile, 2011) and that usually obtained with faces (for a review see Maurer et al., 2002), in the current study we extended the tDCS paradigm used in Civile, Verbruggen, et al. (2016) to the inversion effect for faces. We hypothesized that we would obtain a strong inversion effect for familiar faces in the sham tDCS group, but a significantly reduced inversion effect for familiar faces in the anodal tDCS group because, by analogy

with Civile, Verbruggen, et al.'s (2016) familiar upright checkerboards, we expected anodal tDCS over Fp3 to disrupt recognition performance for familiar upright faces.

Such a result would advance our understanding of both the mechanisms controlling perceptual learning and the face inversion effect in a number of ways. We would have found an experimental procedure (anodal tDCS at Fp3 brain site) able to selectively affect perceptual learning and its expression, and this would help in discriminating between competing theories of this phenomenon. Furthermore, we would have additional evidence that perceptual learning is a contributor (at least in part) to the face inversion effect. Finally, this would be the first demonstration in the literature of how relatively brief tDCS stimulation could reduce our ability to recognize upright familiar faces.

2. Method

We adopted the tDCS montage used in Civile, Verbruggen, et al. (2016). Each subject was randomly assigned to either sham or anodal tDCS conditions. In the sham condition, the tDCS stimulation was only delivered for 30 s, to evoke the sensation of being stimulated, without causing neurophysiological changes that may influence performance. In the anodal tDCS condition, the stimulation was delivered for 10 min commencing just before the subjects began the study phase and lasting for the entire duration of an *old/new recognition* computer task that used images of faces. In both sample groups, the sham and tDCS stimulation started when the computer task began. In the first part of the computer task, the *study phase*, subjects were asked to memorize a set of upright and inverted faces presented one at a time. Following this, subjects were given a *recognition task* where they pressed one key if they thought they had seen the face before, and another key if they thought they had not seen the face before. All the faces seen in the study phase were presented again intermixed with an equal number of new faces of each type (i.e. upright faces, and inverted faces). This *old/new recognition task* is a standard method of assessing face processing and the inversion effect (Civile, McLaren, & McLaren, 2014, 2016; Diamond & Carey, 1986; Yin, 1969). Our main measure was *accuracy* scores during recognition converted into signal-detection d' . We also examined reaction time responses to check for any speed-accuracy trade-off that could affect our interpretation of the results.

2.1. Subjects

Forty-eight students (39 women; mean age = 18.9, age

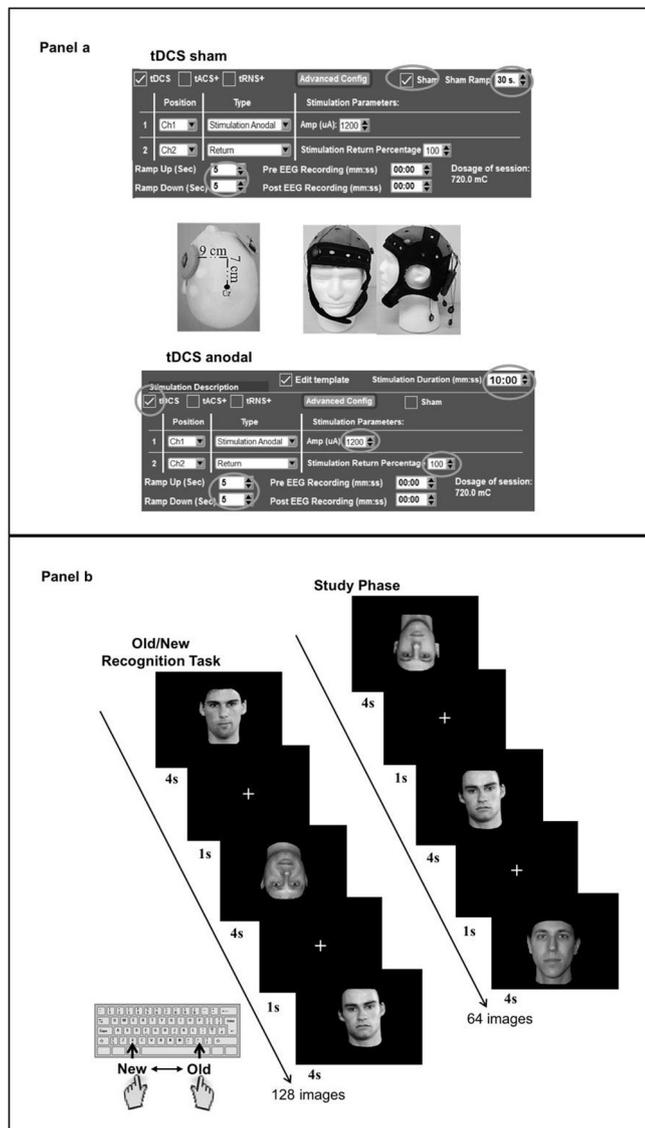


Fig. 2. Panel a shows the electrode configuration of the tDCS and the stimulation set up on the Neuroelectronics software (NIC). Panel b shows the structure of the trials presented during the *old/new recognition* task.

range = 18–22 years) from McMaster University participated in this experiment. Twenty-four subjects were randomly assigned to each of two groups (sham tDCS, anodal tDCS). All subjects were right-handed and were given course credits for their participation. The experiment was approved by the research ethics committee at McMaster University. Written informed consent was obtained after the nature and possible consequences of the study were explained. Sample size was determined in advance based on previous studies (Civile, Zhao, et al., 2014; McLaren, 1997) that found the original inversion effect for checkerboards and that showed a clear effect of tDCS on perceptual learning (Civile, Verbruggen, et al., 2016; McLaren et al., 2016), as well as previous studies that adopted the same old/new recognition task and face stimuli that we used here (Civile, McLaren, et al., 2014, 2016) obtained a strong face inversion effect with group samples of 24 subjects). Additionally, we conducted a post hoc power analysis using G*power software (Faul, Erdfelder, Lang, & Buchner, 2007) that revealed a statistical power of 0.92, better than the recommended 0.80 level of power (Cohen, 1988).

2.2. Materials

The study used 128 images of male faces (pics.stir.ac.uk). Only male faces were used because they allowed the inclusion of ears in the images as well. Men tend to have shorter hair with ears visible whereas women often have longer hair covering the ears, making the visibility of these features rather variable. The faces were standardized in gray-scale format and cropped around the hairline in Adobe Photoshop. The same set of faces was previously used in studies that adopted the same *old/new recognition* task with upright and inverted faces that we used in the study reported here (Civile, McLaren, et al., 2014, 2016).

2.3. Transcranial direct current stimulation (tDCS)

All participants first completed a brain stimulation safety screening questionnaire. Stimulation was delivered by a battery driven, constant current stimulator (Neuroelectronics) via a pair of surface sponge electrodes (25 cm²), soaked in a saline solution (0.9% NaCl), and applied to the scalp at the target areas of stimulation. Electrodes delivered a constant current of 1.2 mA (current density: 0.048 mA/cm²); the choice of the intensity is in line with Civile, Verbruggen, et al. (2016)'s study (see Neuroelectronics website for a review of clinical studies that suggest keeping the average current densities in electrodes below 0.06 mA/cm²). As in Civile, Verbruggen, et al. (2016)'s study, we adopted a bilateral bipolar-non-balanced montage with one of the electrodes (anode/target) placed over the left PFC (Fp3) and the other (Ambrus et al., 2011; Kincses, Antal, Nitsche, Bártfai, & Paulus, 2003) was placed on the forehead, just above the right eyebrow (see Fig. 2, Panel a). In the anodal tDCS condition, the current was applied for 10 min (fade-in and fade-out of 5 s) from when the subjects began the computer task and throughout the *old/new recognition* task. Sham received the same 5 s fade-in and fade-out, but only 30 s stimulation between them, which terminated shortly after the computer task started. The electrodes were left on the participant throughout the experiment.

2.4. Behavioral task

The *old/new recognition* task consisted of two parts: a 'study phase' and an 'old/new recognition phase' (Civile, McLaren, et al., 2014, 2016). In the study phase, each subject was shown upright and inverted faces with 32 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.

2.5. 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 1 s. After this, one of the faces was presented on screen for 4 s. The next trial started with the presentation of a fixation cross again. After all 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 4 s during which time subjects had to respond. The experiment was implemented using SuperLab 4.5 installed on a PC (Fig. 2, Panel b).

2.6. Data analysis

Our primary measure was performance accuracy in the two recognition tasks. The data from all the participants was used in the signal

detection d' analysis of the recognition task (based on performance of both old and new stimuli for each stimulus type) where a $d' =$ of 0.00 indicates chance-level performance (Stanislaw & Todorov, 1999). Each p -value reported in this paper is two-tailed, and we also report the F or t value along with measures of variability (SE or SEM) and effect size (Cohen's d followed by the 95% confidence interval [CI] for d). The study had a 2×2 mixed model design using as a within-subjects factor *Face Orientation* (upright or inverted) and the between-subjects factor *tDCS* (sham or anodal). Follow up, paired t test analyses were conducted to compare performance on upright and inverted faces (the inversion effect) in each tDCS group (sham, anodal). We also assessed performance against chance (d' of 0) to show that both upright and inverted faces in the tDCS sham and anodal groups were recognized (for all four conditions we found $p < .001$ for this analysis).

Statistical analysis of the response latencies was also conducted and no speed/accuracy trade-off was found.

3. Results

The statistical analysis (ANOVA) using the factors *Face Orientation* (upright/inverted) \times *tDCS* (anodal/sham) revealed a significant interaction, $F(1, 46) = 7.45$, $MSE = 0.12$, $p = .009$, $d = 0.78$, $CI = 0.98$, 0.58 . We decomposed the interaction by looking at the inversion effect (upright faces – inverted faces) in each tDCS group (sham, anodal) separately. Following Civile, Verbruggen, et al.'s (2016) study, we expected to find the usual inversion effect for faces in the tDCS sham group. As predicted, a planned comparison showed a significant inversion effect with upright faces ($M = 1.09$, $SE = 0.11$) being recognized significantly better than inverted faces ($M = 0.35$, $SE = 0.07$), $t(23) = 7.48$, $SE = 0.09$, $p < .001$, $d = 1.59$, $CI = 1.78$, 1.41 . Critically, we found a reduced (but still significant) inversion effect in the tDCS anodal group, recognition of upright faces ($M = 0.78$, $SE = 0.11$) compared to inverted faces ($M = 0.44$, $SE = 0.08$), $t(23) = 3.19$, $SE = 0.11$, $p = .004$, $d = 0.69$, $CI = 0.89$, 0.49 (see Fig. 3). Thus, the inversion effect in the tDCS sham group was significantly greater than that in the tDCS anodal group, a similar result to that previously found in Civile, Verbruggen, et al. (2016)'s study using prototype-defined categories of familiar checkerboards.

Importantly, in Civile, Verbruggen, et al. (2016)'s study (Experiment 1) statistical analysis showed recognition of upright familiar checkerboards in the tDCS anodal group was reduced compared to that for familiar checkerboards in the tDCS sham group. We computed an additional analysis in our study to directly compare the recognition

performance for upright faces in the two tDCS groups (sham, anodal). The results were that recognition for upright faces in the tDCS anodal group was reduced compared to that in the tDCS sham group, $t(46) = 1.95$, $SE = 0.14$, $p = .056$, $d = 0.56$, $CI = 0.78$, 0.34 , a result that would be significant on a 1-tailed test. Thus, in both Civile, Verbruggen, et al. (2016)'s study (Experiment 1) and in our current study, we have some evidence that anodal tDCS may affect the recognition of upright familiar stimuli (checkerboards in Civile, Verbruggen, et al. (2016), and faces in the current study). We calculated the Bayes factor using the procedures outlined by Dienes (2011) for this effect with faces using the effect for checkerboards in Civile, Verbruggen, et al. (2016)'s study (Experiment 1) as the prior, setting the standard deviation of p (population value |theory) to the mean for the difference between recognition for familiar upright checkerboards in the tDCS sham group vs that in the tDCS anodal group (0.359). We used the standard error and the mean difference for tDCS sham upright faces vs tDCS anodal upright faces effect found in our study, and assumed a one-tailed distribution for our theory and a mean of 0. This gave a Bayes factor (B) of 3.65. This factor is greater than 3, providing good support for this component of the reduction in the inversion effect (for Bayes factor calculator see Dienes, 2011).

Statistical analysis (ANOVA) of the response latencies was also conducted. Simple comparisons showed a significant inversion effect for both Anodal ($p < .001$) and Sham ($p = .009$) groups, and the inversion effect was numerically larger for the Anodal group, but no significant interaction ($p = .63$) was found. For completeness, we report the mean latencies for each stimulus condition: Sham upright faces, 1.37 s; Sham inverted faces, 1.47 s; Anodal upright faces, 1.48 s; Anodal inverted faces, 1.61 s.

We also report here the SDT Bias estimates for each of the four stimulus' conditions: Sham upright faces, $\beta = 1.33$; Sham inverted faces, $\beta = 1.12$; Anodal upright faces, $\beta = 1.70$; Anodal inverted faces, $\beta = 1.04$.

Finally, for correctness we also reported the statistical analysis for the raw accuracy scores which confirmed the effects showed by our d' prime analyses. As well as for d' , the raw scores revealed a significant interaction $F(1, 46) = 15.12$, $MSE = 3.19$, $p < .001$, $d = 1.04$, $CI = 2.05$, 0.03 . Hence, we recorded a robust inversion effect in the sham group with upright faces ($M = 22.16$, $SE = 0.59$) being recognized significantly better than inverted faces ($M = 18.04$, $SE = 0.37$), $t(23) = 7.88$, $SE = 0.50$, $p < .001$, $d = 1.69$, $CI = 2.66$, 0.71 . A reduced inversion effect for the anodal group was found, with upright faces ($M = 20.25$, $SE = 0.52$) being recognized better than the inverted faces ($M = 18.68$, $SE = 0.49$), $t(23) = 3.06$, $SE = 0.52$, $p = .005$, $d = 0.62$, $CI = 1.62$, -0.37 .

4. Discussion

We adopted the same procedures used in Civile, Verbruggen, et al. (2016) employing the old/new recognition task for faces that is a standard in the literature. The results indicate that anodal tDCS impaired recognition performance for upright faces, and as a consequence, the inversion effect was significantly reduced compared to the usual inversion effect found with faces that can be seen in the sham condition. This is the same effect found with checkerboards in Civile, Verbruggen, et al. (2016), and so strengthens the case for the perceptual learning effect in those experiments and in Civile, Zhao, et al. (2014) contributing to the face inversion effect in this study.

We also argued in our introduction that if we were to find this effect, then it would help us choose between theories of perceptual learning. In our earlier papers, we have noted that the MKM model (McLaren, Kaye, & Mackintosh, 1989) and its later development in McLaren and Mackintosh (2000) and McLaren, Forrest, and McLaren (2012) can explain the inversion effects reported by McLaren (1997) and Civile, Zhao, et al. (2014) because it predicts that perceptual learning will occur as a consequence of experience with (pre-exposure to) the

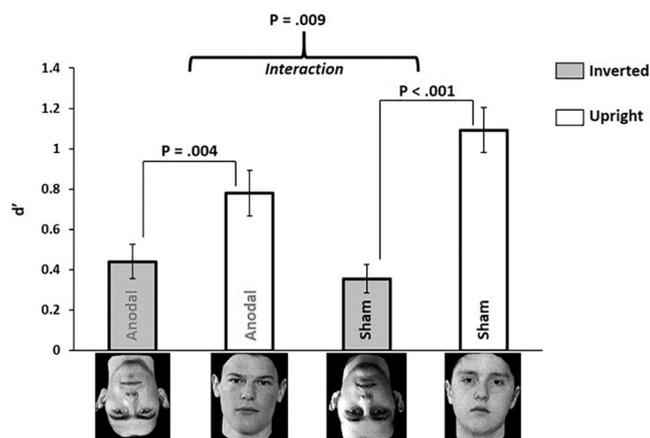


Fig. 3. The y-axis gives d' means for the old/new recognition task (higher = better, 0 = chance), and the different stimulus' conditions in the two tDCS groups (sham, anodal) are shown on the x-axis using typical stimuli from the experiment. The actual dimensions of the stimuli were 6.95 cm \times 5.80 cm. Participants sat 1 m away from the screen on which the images were presented. Error bars represent s.e.m.

category. But most models of perceptual learning would make that prediction. Where we have been able to go further is in pointing out that if the salience modulation based on prediction error implemented by the MKM model is disrupted (and we argue that this is what anodal tDCS to Fp3 does), then the MKM model turns into one more akin to McClelland and Rumelhart's (1985) model of categorization, and enhanced generalization between exemplars as a consequence of familiarity with that category is predicted rather than the enhanced discriminability that is the hallmark of perceptual learning. The result is the elimination of the inversion effect seen with artificial stimuli (that we take to be entirely due to perceptual learning), and even some reversal of the perceptual learning effect, explaining the pattern observed by Civile, Verbruggen, et al. (2016).

Our present data, however, imply that anodal tDCS to Fp3 applied during pre-exposure not only affects perceptual learning for artificial stimuli (the checkerboards in Civile, Verbruggen, et al., 2016) that were novel until encountered in the experimental setting, but can also affect the long established perceptual learning for faces that is a result of experience over many years. This is a truly striking result that suggests that perhaps anodal tDCS over Fp3 may prevent individuals from exploiting "expertise" when called on to discriminate between stimuli of a class they are very familiar with. As far as we are aware, only the MKM model actually makes this prediction, i.e., only the MKM model can explain why this tDCS manipulation can affect established perceptual learning. Other models may be able to explain why it would disrupt the effects of pre-exposure and stop perceptual learning developing, but the MKM model, by postulating a radical change in the way the connectionist network operates as a consequence of tDCS to Fp3, can explain why the expression of previous learning can also be affected. Put simply, the associations between representational elements that are the basis of the exposure learning that takes place and leads (in normal circumstances) to enhanced discriminability remain unaffected. So the representation of experience is unchanged. But its expression, the effect it has in modulating the salience (the activation) of those same representational elements is changed. Instead of highly predicted elements (strong associations to them) having low salience, they now have high salience, and it is this change that undermines the inversion effect. Previously, experience with the category resulted in the elements corresponding to the unique or distinctive (non-prototypical) features of the exemplar being relatively more salient (than those corresponding to the prototypical features), aiding discrimination and helping participants tell one exemplar from another during the recognition phase. But after anodal tDCS, these individuating elements are now relatively less salient than those common to many faces. The upshot is that performance on upright faces suffers because these are the stimuli drawn from the category (upright faces) that our participants have experience with. Inverted faces are less affected, as they benefit less from perceptual learning.

We have argued that these data strengthen the analogy between our checkerboard experiments and those with faces. In both cases, anodal tDCS reduces the inversion effect, and reduces performance on upright exemplars taken from a familiar category. This suggests that the inversion effect obtained with what were novel, artificial stimuli, and that we attribute to perceptual learning, is at least one component of the face inversion effect. True, the inversion effect was completely eliminated by anodal stimulation in Civile, Verbruggen, et al. (2016), but is still present in our stimulation group when we use faces. This could mean that any disruption of perceptual learning (which might be expected to be stronger after many years of experience) is less complete in the current experiment, or it might be that there is a component of the face inversion effect that is not due to perceptual learning. We cannot say at present. What we can say is that the theory we have of how anodal tDCS to Fp3 works predicted a reduced inversion effect, and our salience modulation via error account of perceptual learning is, to that

extent, further validated. We have also shown that we can turn perceptual learning in humans on and off, which opens the door to future applications.

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