

Modulating Perceptual Learning Indexed by the Face Inversion Effect: Simulating the Application of Transcranial Direct Current Stimulation Using the MKM Model

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We report here two large studies investigating the effects of an established transcranial direct current stimulation (tDCS) procedure on perceptual learning as indexed by the face inversion effect. Experiments 1a and 1b ($n = 128$) examined the harmful generalization from Thatcherized faces to normal faces by directly comparing the size of the inversion effect for normal faces when presented intermixed with Thatcherized faces (Experiment 1a) versus that obtained when normal faces were presented intermixed with checkerboards (Experiment 1b). The results from the sham/control tDCS groups provide the first direct evidence in the literature showing how Thatcherized faces generalize onto normal ones producing a reduced inversion effect compared to when normal faces are presented with stimuli (e.g., checkerboards) that do not generalize significantly to normal faces. In the anodal tDCS groups, this effect was reversed, with a larger inversion effect recorded for normal faces in Experiment 1a versus that found in Experiment 1b. Further analyses within each experiment confirmed that the anodal tDCS procedure can enhance the inversion effect for normal faces in circumstances where harmful generalization would otherwise be produced by the Thatcherized faces (Experiment 1a). We also demonstrated our standard reduction in the inversion effect for normal faces consequent on the application of tDCS when presented intermixed with stimuli that do not generalize onto them. We interpret our results in terms of simulations using the MKM model of perceptual and associative learning.

Keywords: perceptual learning, face inversion effect, face recognition

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In this introduction, we start by outlining the theory and the specific behavioral index (i.e., the face inversion effect) that we use to show how transcranial direct current stimulation (tDCS), can modulate perceptual learning. We then offer the simulation work that we conducted based on the basic McLaren et al. (1989) model of perceptual learning. This is necessary to arrive at the predictions we make for the tDCS experiments conducted in this paper. We begin with the basics of perceptual learning as applied to the face inversion effect.

The face inversion effect is one of the most reliable and replicated cognitive phenomena in psychological literature. Several studies have demonstrated that when individuals are presented with inverted

face stimuli (i.e., the faces are upside down), their recognition performance is severely disrupted compared to when they are presented with faces in their usual upright orientation (Civile, McLaren, & McLaren, 2014, 2016; Diamond & Carey, 1986; Farah et al., 1995; Valentine, 1988; Yin, 1969). When it was first discovered the inversion effect was interpreted as evidence in support of the specificity account of face recognition skills. This was because the inversion effect for faces was found to be larger than for other sets of stimuli (e.g., houses, airplanes; Yin, 1969). However, this account was later challenged by the finding that a robust inversion effect like that for faces could be obtained for dog images when the participants were dog breeders suggesting an expertise-based account of face recognition (Diamond & Carey, 1986). Additional support for this idea came from the work conducted by Gauthier and Tarr (1997) revealing an inversion effect for artificial stimuli named Greebles after participants were trained with them, and by McLaren (1997) which revealed a robust inversion effect for artificial prototype-defined categories of checkerboards after familiarization with them.

In recent years, McLaren (1997)'s work has been replicated and extended by Civile, Zhao, et al. (2014). The authors adopted an old/new recognition task paradigm of the kind often used in the face inversion effect literature, and through a series of studies, they demonstrated how a robust inversion effect can be obtained for prototype-defined checkerboards (i.e., all are distortions of one base pattern) that participants had been preexposed to so that the category was familiar. Specifically, the experimental paradigm started with the participants being engaged with a categorization task (this was the preexposure phase) where they were asked to classify by

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trial and error (with feedback) a set of checkerboards drawn from two prototype-defined categories. Following this, a study phase was presented, where new checkerboards drawn from one of the two familiar categories (one of the categories seen in the categorization task) were presented intermixed with checkerboards drawn from a novel category not seen previously in the categorization task. Participants were asked to memorize them. Importantly, some of the checkerboards drawn from the familiar category were presented upright and some others rotated by 180° (i.e., inverted). Because checkerboards are nonmono-orientated stimuli (i.e., they do not have one pre-defined orientation), the upright orientation consisted of the same orientation that participants were familiarized with during the categorization task. For the checkerboards drawn from a novel category, no real upright or inverted orientations existed because participants were never familiarized with the prototypical white distribution of black and white squares for that novel category. The final phase involved an old/new recognition task where the same checkerboards seen during the study phase were presented again intermixed with new exemplars split by the same stimulus conditions (familiar/novel, upright/inverted). The results revealed a robust inversion effect for the checkerboards drawn from a familiar category, no inversion effect was found for those drawn from a novel category (Civile, Zhao, et al., 2014; for pilot work see also McLaren & Civile, 2011).

The results obtained by Civile, Zhao, et al. (2014) were explained using the MKM theory of perceptual learning (first devised by McLaren et al., 1989; further refined by McLaren & Mackintosh, 2000; McLaren et al., 2012). This theory, and its implementation as a model, is based on the modulation of salience by error to produce the type of perceptual learning underpinning the inversion effect for checkerboards seen in Civile, Zhao, et al.'s (2014) work and by extension the face inversion effect. The MKM model is parameterized so that if the features (or units) determining a stimulus are well predicted by other features (i.e., low error), then these features have lower salience (i.e., activation). However, features that are not well predicted, for example, because they are novel, have higher salience. This approach gives rise to perceptual learning for discrimination between AX and BX when these stimuli are preexposed because the common features X would be better predicted as a consequence of preexposure than the unique features A and B, and so have lower salience than the unique features. Thus, the generalization between AX and BX via the common features X would be reduced because of the X features relatively low salience during learning and performance. We can extend this idea to prototype-defined categories of stimuli, where the prototype could be taken as the set of common, X features, and the distinctive features of each exemplar, as unique features that would differ from one another for different exemplars. Familiarity with such a category will lead to reduced generalization between exemplars. This is because the influence of the X features that each exemplar possesses will be diminished by the reduction in salience contingent on exposure to the category. This would lead to perceptual learning because the salience of the unique features (distinctive in each exemplar) would be relatively high resulting in improved discrimination.

Coming back to Civile, Zhao, et al.'s (2014) results, during the categorization task participants must associate the category prototypical/common features shared by the exemplars with the correct category. These common features would rapidly lose their salience because they are presented on every trial and so become well-predicted and slow to form new associations. This would lead to

perceptual learning because the features unique to each checkerboard would still have relatively high salience due to less exposure and lower predictability. Thus, when asked to memorize and then recognize the checkerboards it is easier for the participants to do so because the salience of the common features is now low, whereas that of the unique features is still high. This process of feature salience modulation applies only to upright checkerboards because the participants would have less experience in seeing inverted ones and so performance on these is not aided by any significant amount of perceptual learning. We can then apply this analysis to faces. Because of our experience with upright faces, the features common to those faces, become strongly associated with one another reducing their error scores, and the salience (activation) of the units representing those features would decline. But the novel and unpredicted features that tend to be specific to a given face do not suffer from this salience reduction. Thus, these "unique" features would stand out and would be more available for learning, leading to improved discrimination/recognition between upright faces. However, when faces are inverted, this learning mechanism based on previous experience would no longer apply because the unfamiliar spatial arrangement of features renders those features less well predicted by other features, and this would interfere with the differential salience modulation that is ordinarily in place between common and distinctive features of upright faces.

It is important to note that other approaches to perceptual learning would not be able to explain the results obtained from the checkerboard inversion effect paradigm developed by Civile, Zhao, et al. (2014). For instance, previous work demonstrated that in some circumstances perceptual learning would involve participants learning where exactly to look (i.e., a form of selective attention) rather than involving enhancement of stimulus discriminability (Jones & Dwyer, 2013; Wang et al., 2012). Hence, it could be argued that the better performance for the familiar upright checkerboards would be due to participants learning during the categorization task where to look for the specific location of the features. However, in Civile, Zhao, et al. (2014) the checkerboards were randomly generated and there was no specific location to focus on to individuate the unique features. The squares changed varied from checkerboard to checkerboard making any strategy of learning where to look for the unique features in a specific location unlikely to succeed. Similarly, a standard connectionist category learning approach would not explain Civile, Zhao, et al.'s (2014) findings as the McClelland and Rumelhart (1985) model would predict that the common features of a prototype-defined stimulus form the strongest associations to an outcome. In this case, individuals preexposed to prototype-defined stimuli would become worse at discriminating new exemplars drawn from the familiar categories due to the common features between the exemplars and the category prototype becoming the most salient as a result of their greater activation based on greater net input. This would lead to increased generalization rather than to the perceptual learning effect found in Civile, Zhao, et al. (2014).

With the aim of creating a direct link between the checkerboard inversion effect, the index of perceptual learning, and the face inversion effect, a recent line of research applied tDCS to systematically modulate the inversion effect. Using a double-blind, between-subjects design, it has been shown that anodal tDCS targeting the dorsolateral prefrontal cortex (at the Fp3 scalp site for a 10 min duration at 1.5 mA intensity) delivered during the preexposure phase

(i.e., the categorization learning task), eliminates the checkerboard inversion effect (Civile, Verbruggen, et al., 2016). In particular, recognition performance for upright familiar checkerboards was disrupted compared to that in the sham/control tDCS group. In the sham group, the results confirmed the robust checkerboard inversion effect for a familiar category previously established in the literature by Civile, Zhao, et al. (2014). The same anodal tDCS procedure was then extended to the face inversion effect old/new recognition paradigm. Critically, the authors found a significant reduction of the face inversion effect in the anodal group compared to the sham group when the tDCS was delivered during the learning phase (i.e., the study phase) or during the recognition phase confirming the immediate effect of the tDCS on the inversion effect. In this case, as well, the reduction of the inversion effect was due to an impaired recognition performance for upright faces induced by the anodal stimulation (Civile, McLaren, et al., 2020; Civile, McLaren, & McLaren, 2018). This is an established result that has been replicated in several papers (Civile, Cooke, et al., 2020; Civile et al., 2019; Civile & McLaren, 2022; Civile, McLaren et al., 2021; Civile, Quaglia, et al., 2021; Civile, Waguri, et al., 2020). It is also important to highlight that across several studies the authors have selectively tested the tDCS-induced effects when delivered at the start of the categorization task (Civile, Verbruggen, et al., 2016), the study phase (Civile et al., 2019; Civile, McLaren, & McLaren, 2018; Civile, Waguri, et al., 2020), the recognition phase (Civile, McLaren, et al., 2020), or at the start of a matching task (Civile, Quaglia, et al., 2021). The outcome was always to confirm that the tDCS procedure reduces the inversion effect by affecting performance for upright stimuli. In addition to the sham control, the authors have also conducted *active control* studies addressing the issue of whether the modulation of the inversion effect induced by the tDCS procedure could be obtained by targeting different brain areas. The results confirmed that the reduction of the inversion effect is not obtained in these circumstances (Civile, McLaren, et al., 2021; Civile, McLaren, & McLaren, 2018).

The explanation suggested for the effects of tDCS on the inversion effect derives from the MKM model, specifically when the anodal tDCS procedure is used, the reduction of the inversion effect for checkerboards and for faces would be due to impaired recognition performance for upright stimuli because of the disruption of feature salience modulation. This follows from the assumption that the anodal stimulation disables the mechanism for salience modulation based on error, which means that instead of prior preexposure to a prototype-defined category enhancing the discriminability of the exemplars taken from that category, it now, if anything, enhances generalization between them. Features common to exemplars would be more prominent because they coactivate one another, whereas unique features found in one or very few exemplars would have low salience as they do not receive additional activation. It is this change in perceptual learning that causes the reduction in the inversion effect because it reduces participants' ability to discriminate between different upright faces, essentially making the faces look more "similar" to one another. Importantly, this explanation was confirmed when the same tDCS procedure was applied in a prototype-distortion task where increased salience of the prototypical features would lead to improved task performance. Here, the tDCS procedure applied to a categorization task involving prototype-defined checkerboard exemplars, improved performance when, later, subjects categorized the prototypes which had not

been presented before, apparently enhancing their ability to extract the common features shared between the exemplars and the prototype (McLaren et al., 2016).

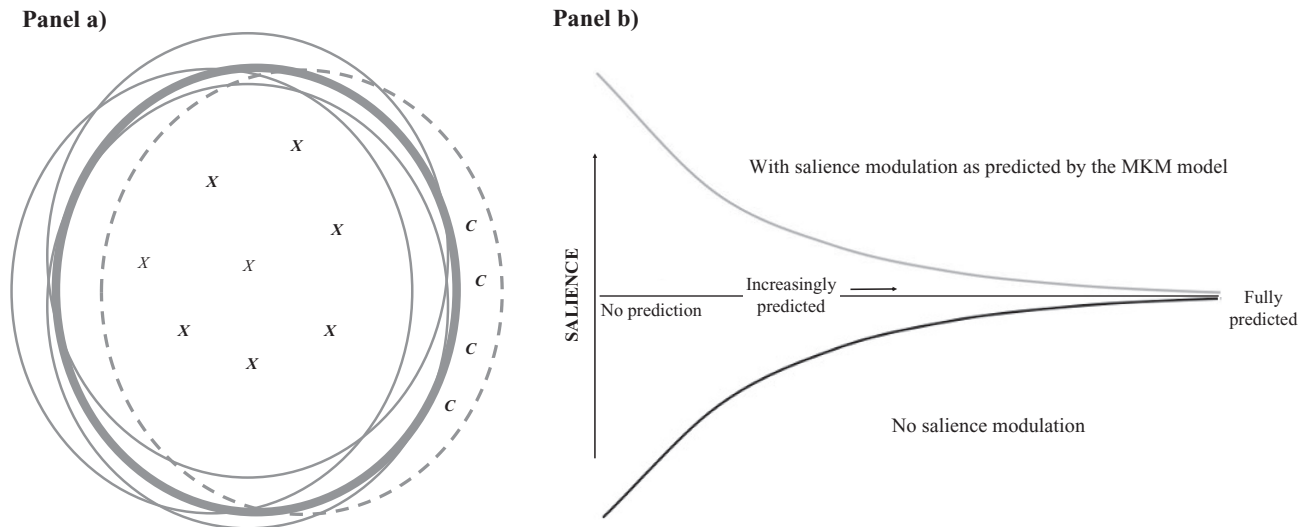
To illustrate this, Figure 1 shows a schematic representation of feature salience modulation in the MKM model under normal circumstances and when our tDCS procedure is assumed to apply. Panel a illustrates (dashed circle) one category exemplar that possesses common features (x) that it shares with other category exemplars, and its unique features (c). Panel b instead illustrates how salience modulation would change based on the MKM model because of exposure to category exemplars (top curve in gray). The associations among x features and between c and x features quickly form and, therefore, the salience of the x features falls quickly. The relatively novel c features would not be so affected by this decline in salience, and so would become relatively salient, making it easier to learn about each exemplar. The lower curve (black line) shows how salience would change if error-based modulation was not in operation because of the influence of tDCS. In this case, as associations between elements form, salience increases rather than decreases, because the associations between features contribute to the total activation of each feature. This means that the common, x features would be at an advantage in terms of salience compared to the unique, c features. Thus, this would help learning about the commonalities between the exemplars rather than the differences.

Further evidence on how tDCS affects the perceptual learning component of face recognition comes from recent work where the same tDCS procedure delivered at Fp3 was used to *enhance* the inversion effect. The work in question employed normal faces presented either with other normal faces or with Thatcherized faces (Civile, Cooke, et al., 2020). Through a series of experiments where participants were engaged in an old/new recognition task involving upright and inverted normal and Thatcherized faces presented intermixed, the authors provided evidence in support of the anodal tDCS procedure being able in some circumstances to increase the inversion effect for normal faces through means of increased recognition performance for upright faces compared to sham. The authors confirmed that the anodal tDCS procedure, as has typically been the case, was able to significantly reduce the inversion effect compared to the sham when normal faces were presented with other normal faces (male and female faces). But when normal faces were presented with Thatcherized faces (male normal and Thatcherized faces) the inversion effect for normal faces was significantly increased by application of the same tDCS procedure (Civile, Cooke, et al., 2020). Civile, Cooke, et al. (2020) interpreted their results based on the MKM model. Hence, they suggested that when normal faces are presented intermixed with Thatcherized faces, the tDCS procedure reduced the harmful effect of generalization from Thatcherized to normal faces thus leading to an increased face inversion effect for normal faces. To understand this analysis, we first need to understand what Thatcherized faces are and how they might be represented.

Thatcherized faces are a set of specially manipulated faces where the eyes and mouth have been rotated by 180° while the rest of the face remains upright. The result is a face that, when it is presented upright, the rotated eyes and mouth stand out as rather "odd" and salient, however, if inverted, the manipulated features are not so easily apparent. This effect is known as the "Thatcher Illusion" (Civile, Elchlepp, et al., 2018; Civile et al., 2011, 2012; Civile, McLaren, &

Figure 1

Panel a Illustrates How a Prototypical Stimulus (Bold Circle) Can Be Represented as a Set of Features, and How That Set Changes When the Prototype Is Distorted to Produce Exemplars (Other Circles) That Share Common Features (*x*) and Have Their Own Unique Features (*c*). Panel b Shows How Element Salience Changes in the MKM Model as Associations Are Formed (Top Curve in Gray) and How It Would Change Without Modulation of Salience (Bottom Curve in Black) Induced by the Application of the tDCS Procedure



Note. tDCS = transcranial direct current stimulation.

McLaren, 2016; Lewis, 2001; Lewis & Johnston, 1997; Thompson, 1980). Just as normal faces have features that are either distinctive or common, so do Thatcherized faces. But for Thatcherized faces, some of the common (*x*) and unique (*c*) features of normal faces would have been changed and some left unaltered. Some of the changed features would be common to Thatcherized faces (*t*) and unique to a specific Thatcherized face (*u*). Based on the MKM, the *t* features will be shared across other Thatcherized faces, and they will be very salient, because the predictions made by other features of the face will be incorrect. They will be predicting a mouth or the eyes that are the right way up, not inverted. This will make the *t* features seem super-novel, and hence very salient determining their odd look. As such, they will be learned rapidly, and this will make it hard to discriminate between upright Thatcherized faces. As consistently demonstrated in the face recognition literature, in circumstances where tDCS is not applied, the net result is a smaller inversion effect for Thatcherized faces due to a reduction in recognition performance for upright faces (Civile, Cooke, et al., 2020; Civile, Elchlepp et al., 2018; Civile et al., 2011, 2012; Civile, McLaren, & McLaren, 2016; Maurer et al., 2002; Rakover, 1999).

Importantly, the MKM model also predicts that performance for normal upright faces would be affected by presenting the Thatcherized upright faces. This is because Thatcherized faces contain features in common with normal faces (e.g., eyes and mouth) which are more salient in the Thatcherized faces (they are now relatively unpredicted), and so they capture more of the learning, and this then generalizes to normal upright faces making recognition for them harder. Presenting upright Thatcherized faces with upright normal faces, would make a performance for the normal faces worse, however, there would not be a symmetric effect of generalization from normal to Thatcherized faces, because the same features (e.g., eyes and mouth) in normal upright faces are

simply not as salient as the super-salient ones in Thatcherized faces. And equally, there would be unaltered features in an upright Thatcherized face that are common to all faces (e.g., the nose). These will, of necessity, become more salient because of Thatcherization, due to many of the features predicting them (and lowering their error) having themselves changed. This will have an impact in promoting generalization from upright Thatcherized faces to upright normal faces, making discrimination between them more difficult. Overall, the basic idea behind this prediction is that generalization from upright Thatcherized faces would lead to a reduced recognition performance for upright normal faces in the sham condition, reducing the inversion effect, and that anodal tDCS releases the upright normal faces from this effect and so would enhance the inversion effect.

In this article, we aim to directly demonstrate in the same study how adding Thatcherized faces into the mix would induce the harmful effects of generalization on normal faces leading to a reduced inversion effect (Experiment 1a) compared to when the same normal faces would be presented intermixed with stimuli (i.e., checkerboards) that do not generalize onto them (Experiment 1b). In the anodal tDCS groups, based on previous work (Civile, Cooke, et al., 2020), we expected the tDCS procedure to change this by producing an increased inversion effect for normal faces when presented intermixed with Thatcherized faces (Experiment 1a), and a reduced inversion effect for normal faces when presented intermixed with checkerboards (Experiment 1b). Key to our investigation is the simulations that guided our predictions for this experimental work. We start by reporting a summary of the modeling and results with additional details given in the [online supplemental materials](#) document. Following this, we will give the empirical results which are the main subject of our investigation.

The Modeling

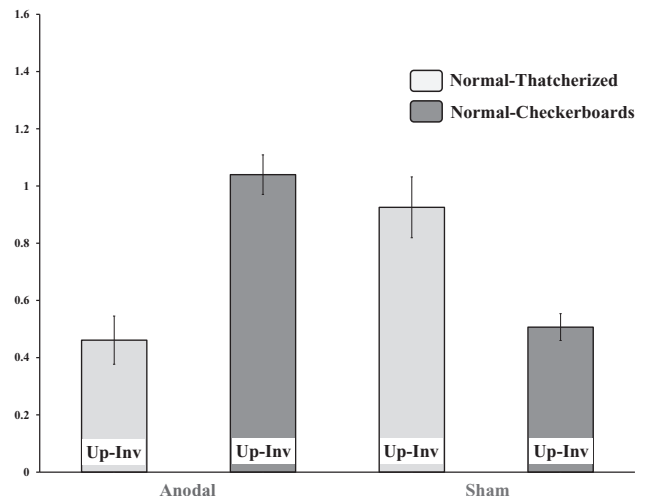
To keep the modeling as straightforward and easily interpretable as possible, we used the original MKM formulation (McLaren et al., 1989) rather than its later variants. The design of the network used for our simulations is as follows. Each stimulus, either a notional “face” or “checkerboard,” is represented by a pattern of activation over 39 input units. All these units are connected to one another and to another unit (unit 40) that serves as a “tag” that stimulus has been seen during the study phase of the old/new recognition experiment. Before the study phase, a set of 900 “normal” faces are experienced by the system to mimic the perceptual experience that participants bring to the experiment (i.e., simulations with prior experience of faces). This is done without any tagging. Then 50 normal faces are shown and tagged, intermixed with either 50 Thatcherized faces or 50 checkerboards (and these stimuli are also tagged). This is the “study” phase of the task. Finally, the seen normal faces and equivalent unseen ones are presented to the network and assessed for their ability to activate the tag unit, and the difference (seen–unseen) is used as an index of recognition performance. Performance on inverted normal faces is estimated by running the simulations without any prior experience of the normal faces before the study phase, making use of the notion that we are not familiar with inverted faces. This was done because this model does not in any way capture the orientation of a face, and so has no ability to represent an inverted face. The face inversion effect index is extracted by subtracting performance for “inverted” faces (i.e., faces with no prior experience) from performance for upright faces (i.e., faces with prior experience).

The faces use the first 20 units to represent them in the system. Some of these are consistently active for most normal faces (the common features) while others vary from exemplar to exemplar (individuating features though not necessarily unique to a stimulus). The checkerboards are simply treated like the faces but use the other 19 units (21–39) so that there is no overlap between their representations and those of faces and hence no generalization between them. Thatcherized faces are represented by changing some of the common features of normal faces to their opposite (a positive input and activation for a unit becomes negative or vice versa) and then allowing similar random variation to that individuating normal faces. When units are not used their activations stay at 0. Hence, our procedure in these simulations was as follows. If we were dealing with upright, normal faces, for which we have expertise, we started with a preexposure phase to mimic life experience with faces. Preexposure was on a random basis and involved 900 face presentations to the network. After this preexposure phase, the study phase took place. This involved showing 50 faces to the model. During this phase, the 40th unit had its external input set to 0.9. This meant that the units active and present would associate to this unit, but any associations from this unit to the others present and active were prevented from forming so that it simply acted as a “tag” rather than part of the representation of the face. There then followed a test phase in which one specimen “seen” and one “unseen” face were presented to the network and the tag activation read. In the case of testing normal faces, the “seen” face is tested with the units external inputs set in a manner consistent with those used during the preexposure and study phases. The unseen face has most of the units set to the same activations, but a few are changed in a way that did not occur during the study phase. The difference in the activations

of unit 40 is taken to indicate how well the network can discriminate between a seen and unseen face. A similar approach was taken for inverted faces except that no initial preexposure phase was given. The effects of tDCS were modeled by simply switching off salience modulation by error in the MKM by setting the “boost” parameter to 0. Then this whole process (preexposure, study, test) was repeated a total of 10 times and averaged to give a more reliable index of performance. We also replicated this process several times to check that the values obtained were not outliers or flukes of some kind. With this procedure, a typical set of simulations is as shown below. Note that the raw outputs are not a simulation of recognition performance in our experimental work because we have not added in the extra (face-specific) component of the inversion effect we have identified that is not dependent on expertise, which for present purposes we assume to be a constant that is simply added to each condition. We also multiply our simulation results by a scale factor in combination with this constant to then generate the results (more details on this scaling are given in the [online supplemental materials](#) document).

As [Figure 2](#) shows, we can see immediately that the simulation gives us the pattern of effects predicted by the analysis of the MKM model. If we start with the sham tDCS conditions which simply use the MKM model as described, then we can see that intermixing normal faces with checkerboards (sham N + C) leads to a higher inversion effect than intermixing normal faces with Thatcherized faces (sham N + T). If we stay with the normal faces intermixed with checkerboards, and now bring in the tDCS manipulation (turning off salience modulation by reducing the error-driven boost to external input to zero) then we see that the effect of that is to reduce the inversion effect (anodal N + C) relative to sham. This is the established tDCS effect with our procedures found in the literature

Figure 2
Results From the Simulation



Note. The face inversion effect index is extracted by subtracting performance for “inverted” faces (i.e., faces with no prior experience) from performance for upright faces (i.e., faces with prior experience). The anodal tDCS effects were modeled by switching off feature salience modulation in the MKM, turning it into something much more like the [McClelland and Rumelhart \(1985\)](#). tDCS = transcranial direct current stimulation.

(Civile, Cooke, et al., 2020; Civile & McLaren, 2022; Civile, McLaren, et al., 2020, 2021; Civile, McLaren, & McLaren, 2018; Civile, Quaglia, et al., 2021; Civile, Waguri, et al., 2020). And finally, we can see that when normal faces are intermixed with Thatcherized faces, the effect of tDCS is quite the opposite, as it now enhances the inversion effect (anodal N + T; Civile, Cooke, et al., 2020). Thus, we have the requisite proof of principle for the predictions made for the current experimental work.

Experiments 1a and 1b

We will now report the methodology and the results of the two empirical experiments that we conducted. The experiments were conducted concurrently, Experiment 1a included images of normal and Thatcherized faces, and Experiment 1b included images of normal faces and checkerboards.

Method

Subjects

In total, 128 naïve (right-handed) subjects (40 male, 88 female; $M_{\text{age}} = 20.7$ years, age range = 18–29) took part in the two experiments. Experiments 1a and 1b each included 64 subjects randomly assigned to either sham or anodal tDCS groups (32 in each group). All the subjects were students from the University of Exeter. All methods were performed in accordance with the relevant guidelines and regulations approved by the Psychology Research Ethics Committee at the University of Exeter. Informed consent was obtained from all subjects.

Materials

Experiment 1a used the same set of 128 faces previously used in Civile, Cooke, et al. (2020). The original images were selected from the Psychological Image Collection at Stirling open database (<https://pics.stir.ac.uk>). All faces were standardized using a gray-scale color on a black background. For all faces, we cropped the hair and the ears. The faces were prepared in four different versions that is, normal upright, normal inverted, Thatcherized upright, and Thatcherized inverted (Figure 3a). The Thatcherized faces were produced by rotating the mouth and each of the eyes individually by 180°. The stimuli, whose dimensions were 5.63 cm × 7.84 cm, were presented at a resolution of 1,280 × 960 pixels.

Experiment 1b used the same normal faces used in Experiment 1a and the same checkerboard exemplars (5.50 cm × 5.50 cm, presented at a resolution of 1,280 × 960 pixels) used in Civile, Zhao, et al. (2014), Civile, Quaglia, et al. (2021), and Civile, Verbruggen, et al.'s (2016) study that adopted the same tDCS procedure applied to old/new recognition task (Figure 3b).

The Behavioral Task

Experiment 1a used the same behavioral task as that used in Civile, Cooke, et al. (2020, Experiment 2) consisted of a “study phase” and an “old/new recognition phase” (Figure 4a). In the study phase, subjects were shown 32 upright and 32 inverted normal and Thatcherized faces in total (16 in each stimulus condition, i.e., normal upright, normal inverted, Thatcherized upright, and Thatcherized inverted) presented one at a time in random order. In each trial of the study

phase, participants saw a fixation cross in the center of the screen, for 1 s, then a face image was presented for 4 s before moving on to the next trial. After all the 64 face stimuli had been presented, the program displayed a set of instructions, explaining the recognition task. In the recognition phase, 64 upright and inverted novel faces, half normal and half Thatcherized, (16 in each stimulus condition) were showed intermixed with the 64 faces seen in the study phase, and all 128 stimuli were presented one at a time in random order. For a given subject, each face image only appeared in one of the four conditions (normal upright, normal inverted, Thatcherized upright, and Thatcherized inverted). Across participant groups each face image was presented in all four stimulus conditions. The faces were each shown for 4 s (preceded by a 1 s fixation cross) and subjects pressed the “.” key if they recognized the face as having been shown in the study phase or pressed “x” if they did not (the keys were counterbalanced across the subjects).

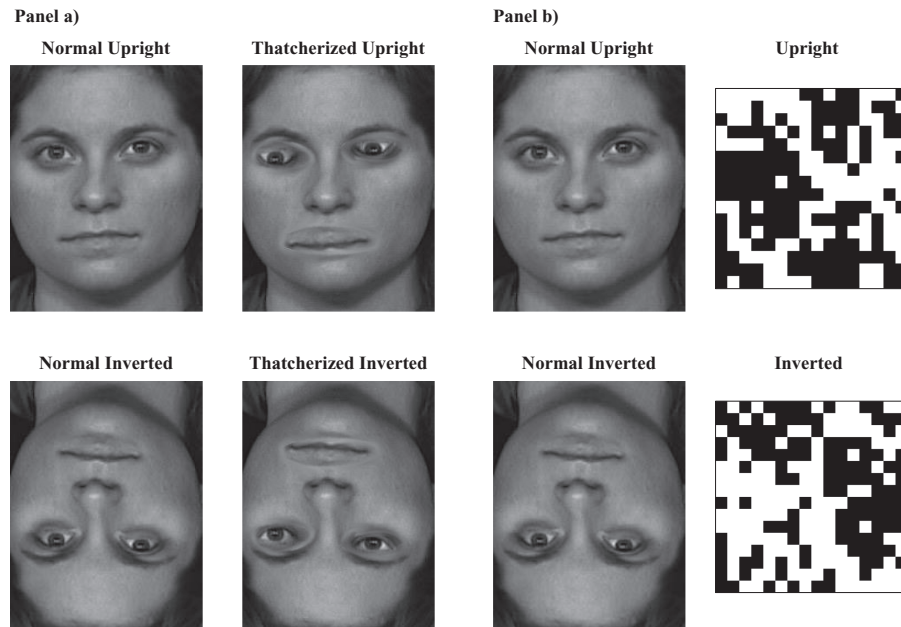
Experiment 1b consisted of a “categorization task,” a “study phase” and an “old/new recognition phase.” As in, Civile, Quaglia, et al.'s (2021), Civile, Verbruggen, et al. (2016), and Civile, Zhao, et al. (2014), subjects were first engaged in a categorization task (the pre-exposure/familiarization phase) where they were asked to sort a set of 128 checkerboards drawn from two prototype-defined categories (64 exemplars in each) presented one at a time in random order. Subjects received immediate feedback as to whether their response was correct or incorrect. If no response was made within 4 s, they will be timed out. The presentation of each checkerboard was signaled by a fixation cross in the center of the screen presented for 1 s. Following this in the study phase subjects were asked to memorize a set of stimuli. The set included 32 checkerboards drawn from one of the familiar categories, 16 of which shown upright and 16 shown inverted. The set also included 16 upright and 16 inverted normal faces drawn from the same set of normal faces used in Experiment 1a. The stimuli were presented one at a time at random order for 4 s intermixed by a fixation cross presented for 1 s. In the old/new recognition phase, 16 upright and 16 inverted new checkerboards drawn from the same familiar category and 16 new upright and 16 inverted normal faces were showed intermixed with the 64 stimuli seen in the study phase (Figure 4b). Essentially, the set of normal faces (images and number of stimuli presented) was the same as in Experiment 1a, but the checkerboard stimuli replaced the Thatcherized faces. All 128 stimuli were presented one at a time in random order. Subjects responded according to whether they thought they had seen the stimuli during the study phase. For a given subject, each face and checkerboard image only appeared in one condition (normal upright or inverted face, familiar upright, or inverted checkerboard). Across participant groups images were presented in all conditions. During the recognition task, the stimuli were each shown for 4 s and subjects pressed the “.” key if they recognized the stimulus as having been shown in the study phase or pressed “x” if they did not (the keys were counterbalanced). The two experiments were conducted concurrently.

The tDCS Paradigm

In both experiments, we adopted the same tDCS montage as that used in previous studies (Civile, Cooke, et al., 2020; Civile & McLaren, 2022; Civile, McLaren, & McLaren, 2018; Civile, McLaren, et al., 2020, 2021; Civile, Quaglia, et al., 2021; Civile, Verbruggen, et al., 2016; Civile, Waguri, et al., 2020), based on a bilateral bipolar-nonbalanced montage with one of the electrodes (anode/

Figure 3

Panel a illustrates an example of the four face conditions used in Experiment 1a. Panel b illustrates an example of the normal faces (same as Experiment 1a) and checkerboard stimuli used in Experiment 1b.



Note. Images of faces are taken from the Psychological Image Collection at Stirling open database (<https://pics.stir.ac.uk>), which are free for research use.

target) placed at Fp3 and the reference was placed on the forehead (above the right eyebrow). In the anodal condition group, a direct current stimulation of 1.5 mA was delivered continuously for 10 min with 5 s fade-in and 5 s fade-out starting as soon as the subjects were ready to begin the experiment (Figure 4c). In both experiments the tDCS was delivered during the study phase. Hence, once the stimulation started the experimenter waited for about 60–90 s to ensure that the subjects felt comfortable with the tDCS. Following the experimenter explained the instruction to the study phase and invited the subjects to press the spacebar to start the task. The stimulation and the study phase ended at about the same time. No stimulation was delivered during the recognition phase (please see Civile, McLaren, et al., 2020, for studies that revealed no differences between tDCS delivered during the study phase vs. the recognition phase only).

Transparency and Openness

Upon acceptance for publication, the data from all experiments in this article will be available on the U.K. Data Service ReShare (<https://reshare.ukdataservice.ac.uk/855016/>). Stimuli and program code can be accessed by contacting the corresponding author c.civile@exeter.ac.uk. The experiments were not preregistered.

Results

Behavioral Data Analysis

In both experiments, the primary measure was the accuracy data from all subjects for the normal faces. These were used to compute a d' sensitivity measure (Stanislaw & Todorov, 1999) for the old/

new recognition task (seen and unseen stimuli for each stimulus type) where a d' of 0 indicates chance-level performance. To calculate d' , we used subjects' hit rate (H), the proportion of SEEN (i.e., "old") trials to which the participant responded SEEN, and false alarm rate (F), the proportion of Not SEEN (i.e., "new") trials to which the participant responded SEEN. The statistic d' is a measure of this difference; it is the distance between the means of the signal + noise and noise alone distributions. Specifically, d' is the difference between the z transforms of the two rates: $d' = z(H) - z(F)$.

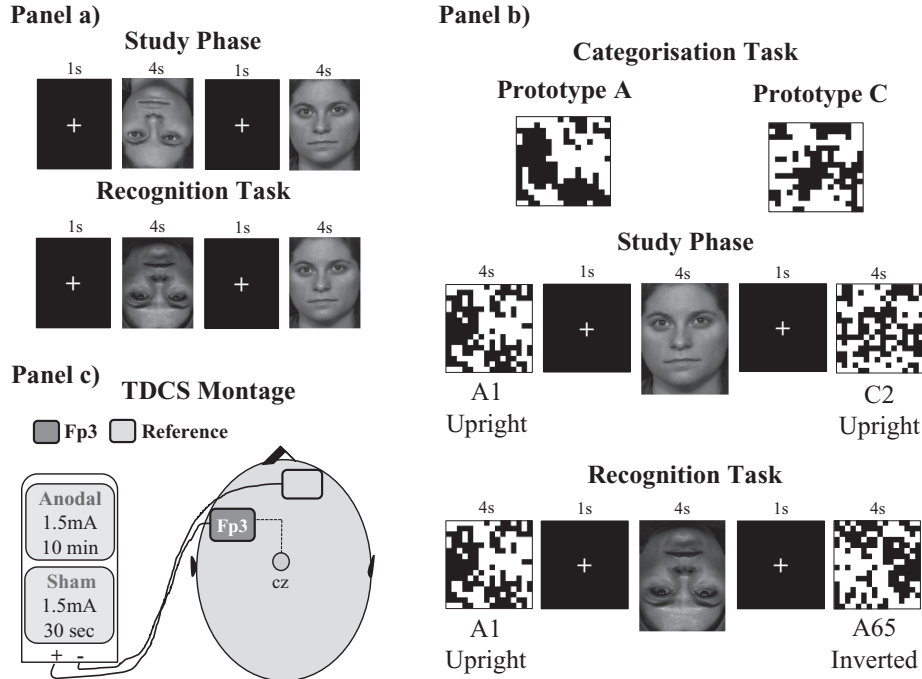
Each p value reported for the comparisons between conditions is two-tailed, and we also report the F or t value along with mean square errors (MSEs) and effect size (η_p^2). In both studies, we assessed performance against the chance to show that normal faces in both the tDCS sham and anodal groups were recognized significantly above chance (for all conditions we found $p < .001$ for this analysis).

It is important to notice that the Thatcherized faces were only used as a manipulation to induce generalization of the normal faces. The checkerboard stimuli were only used to match the number of stimuli presented across the studies and to act as a set of stimuli that does not generalize onto normal faces. Our focus was on (and the predictions were made) the performance of normal faces. However, for completeness, we conducted the analyses also for these stimuli and we report the results in the online supplemental materials document.

Finally, we also provided the results for criterion, C , which were unaffected by our tDCS manipulation. As previously found in the literature the tDCS procedure used here does not influence C for this type of task (see Civile & McLaren, 2022). We report the full analyses in the online supplemental materials document.

Figure 4

Panel a Illustrates the Trial Structure for the Old/New Recognition Task in Experiment 1a. Panel b Illustrates the Base Pattern Prototypes From Which the Checkerboard Exemplars Shown in the Categorization/Preexposure Task Were Drawn From. Furthermore, It Illustrates the Trial Structure for the Old/New Recognition Task Used in Experiment 1b. Panel c Shows the tDCS Montage Used in Both Experiments



Note. tDCS = transcranial direct current stimulation. Images of faces are taken from the Psychological Image Collection at Stirling open database (<https://pics.stir.ac.uk>), which are free for research use.

Results

We computed a $2 \times 2 \times 2$ mixed model ANOVA on the d' scores from the normal faces conditions using as a within-subjects factor, *face orientation* (normal upright or normal inverted), the between-subjects factor *tDCS stimulation* (sham or anodal) and the between-subjects factor *experiment* (1a or 1b). The overall three-way interaction (*Face Orientation* \times *tDCS Stimulation* \times *Experiment*) was highly significant, $F(1, 124) = 12.30$, $MSE = 4.06$, $p = .001$, $\eta_p^2 = 0.09$, indicating that the effects of tDCS on the inversion effect were different in the different experiments. There was a significant main effect of *face orientation* $F(1, 124) = 104.11$, $MSE = 34.41$, $p < .001$, $\eta_p^2 = 0.45$, which reflects the standard inversion effect with better performance to upright faces, and a significant interaction between *Face Orientation* \times *tDCS Stimulation*, $F(1, 124) = 4.60$, $MSE = 1.52$, $p = .034$, $\eta_p^2 = 0.03$. No significant interaction was found between *Face Orientation* \times *Experiment*, $F(1, 124) = 0.260$, $MSE = 0.08$, $p = .611$, $\eta_p^2 < 0.01$, and no significant main effect of the between-subjects factor *tDCS stimulation* was found, supporting the contention that tDCS in our procedure does not simply affect overall performance, $F(1, 124) = 1.26$, $MSE = 0.91$, $p = .26$, $\eta_p^2 = 0.01$.

Using our insights from the simulation work to further investigate these results and understand the basis of the three-way interaction, we conducted an independent sample t test using the inversion effect index (performance for upright–inverted stimuli)

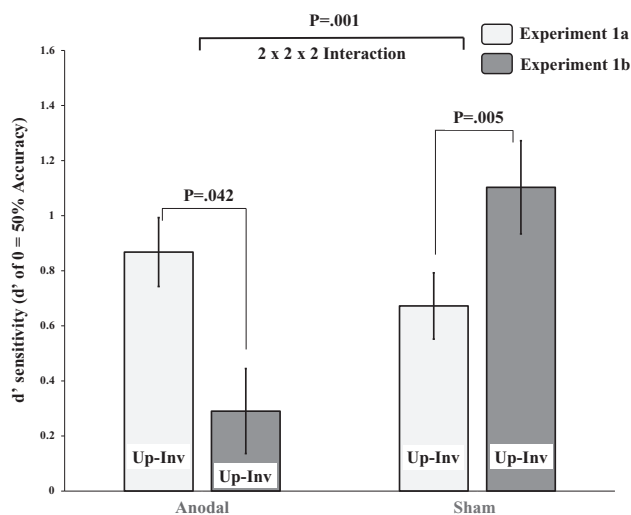
for normal faces from the sham groups which revealed a significantly larger inversion effect in Experiment 1b ($M = 1.10$, $SD = 0.95$) compared to that in Experiment 1a ($M = 0.67$, $SD = 0.68$), $t(62) = 2.07$, $SE = 0.20$, $p = .042$, $\eta_p^2 = 0.13$. The same analysis for the inversion effect for normal faces in the anodal groups revealed a significantly reduced inversion effect in Experiment 1b ($M = 0.290$, $SD = 0.87$) compared to that in Experiment 1a ($M = 0.867$, $SD = 0.70$), $t(62) = 2.90$, $SE = 0.19$, $p = .005$, $\eta_p^2 = 0.26$ (Figure 5).

Additional Analyses Experiment 1a

We computed a 2×2 mixed model design using, as a within-subjects factor, *face orientation* (normal upright or normal inverted), and the between-subjects factor *tDCS stimulation* (sham or anodal), which revealed a significant main effect of *face orientation*, $F(1, 62) = 78.69$, $p < .001$, $MSE = 18.97$, $\eta_p^2 = 0.56$. However, no significant interaction between *Face Orientation* \times *tDCS Stimulation* was found, $F(1, 62) = 1.27$, $MSE = 0.307$, $p = .264$, $\eta_p^2 = 0.02$. Thus, compared to Civile, Cooke, et al. (2020), this time we found that the inversion effect for normal faces when presented with Thatcherized faces was increased but only numerically in the anodal condition ($M = 0.87$, $SD = 0.72$) compared to the sham condition ($M = 0.71$, $SD = 0.65$). No significant main effect of *tDCS stimulation* was found, $F(1, 62) = 1.46$, $MSE = 0.457$, $p = .230$, $\eta_p^2 = 0.02$.

Figure 5

This illustrates the Inversion Effect Index for Normal Faces Across Experiment 1a and 1b



Note. The x-axis gives each tDCS condition in the two experiments. The y-axis gives the inversion effect index which was extracted by calculating the difference in performance for upright-inverted faces using the d' sensitivity measure. Error bars are SEM. tDCS = transcranial direct current stimulation.

Additional Analyses Experiment 1b

We computed a 2×2 mixed model design using, as a within-subjects factor, *face orientation* (normal upright or normal inverted), and the between-subjects factor *tDCS stimulation* (sham or anodal), which revealed a significant main effect of *face orientation*, $F(1, 62) = 36.97$, $MSE = 15.52$, $p < .001$, $\eta_p^2 = 0.37$, and a significant interaction between *Face Orientation* \times *tDCS Stimulation*, $F(1, 62) = 5.28$, $MSE = 5.28$, $p = .001$, $\eta_p^2 = 0.17$. No significant main effect of *tDCS stimulation* was found, $F(1, 62) = 0.285$, $MSE = 0.283$, $p = .595$, $\eta_p^2 < 0.01$. In agreement with earlier work (Civile, Cooke, et al., 2020; Civile, Elchlepp, et al., 2018; Civile et al., 2019; Civile, McLaren, et al., 2020, 2021; Civile, Quaglia, et al., 2021; Civile, Waguri, et al., 2020) we found a significantly reduced face inversion effect in the anodal group, $t(31) = 1.87$, $SE = 0.154$, $p = .069$, $\eta_p^2 = 0.10$, compared to the robust inversion effect found in the sham group, $t(31) = 6.51$, $SE = 0.169$, $p < .001$, $\eta_p^2 = 0.58$. As for previous studies, recognition performance for upright faces was significantly reduced by the anodal tDCS when compared to sham, $t(31) = 2.09$, $SE = 0.228$, $p = 0.04$, $\eta_p^2 = 0.06$.

Additional Bayes Factor Analyses Experiment 1a

We provide a Bayes factor analysis using the procedure outlined by Dienes (2011), aiming to capture the apparent 2×2 interaction in Experiment 1a, using as *priors* the differences found in Civile, Cooke, et al.'s (2020) Experiment 2 (0.29) and 3b (0.32) averaged together (0.30). We used the standard error (0.10) and mean difference (0.20) between the inversion effect in the sham group versus that in the anodal group in Experiment 1a. This gave a Bayes factor of 3.70, which is good evidence (greater than 3, for the conventional

cut-offs see Dienes, 2011; Jeffreys, 1961), in line with previous studies, in support of the tDCS procedure used here increasing the face inversion effect for normal faces when they are presented intermixed with Thatcherized faces.

Additional Bayes Factor Analyses Experiment 1b

This time we provide a Bayes factor analysis aiming to capture the 2×2 interaction in Experiment 1b, using as *priors* the differences found in the original Civile, McLaren, and McLaren (2018) Experiment 1 (0.26) and 2 (0.35) averaged together (0.30). We used the standard error (0.10) and mean difference (0.20) between the inversion effect in the sham group versus that in the anodal group in Experiment 1b. This gave a Bayes factor of 1,762, which is strong evidence that confirms the established that the same tDCS procedure can decrease the inversion effect for normal faces when presented in isolation or intermixed with set of stimuli that do not generalize onto them (e.g., checkerboards).

Finally, we also conducted a Bayes factor analysis using as *priors* the mean difference between sham upright faces and anodal upright faces found in Civile, McLaren, and McLaren (2018) Experiments 1 (0.22) and 2 (0.34) averaged together (0.28). We then used the standard error (0.16) and mean difference (0.50) between sham normal upright faces and anodal normal upright faces in our Experiment 1b. This gave a Bayes factor of 39.33, which is also strong evidence for the position that performance to normal upright faces is reduced by the tDCS procedure when normal faces are intermixed with stimuli that do not generalize onto them.

General Discussion

In this article, we report the results from experiments that directly investigated the tDCS-induced effects on perceptual learning indexed by the face inversion effect as a function of generalization from and modulation by other stimuli present. Previous research has shown how a particular tDCS procedure can selectively modulate the inversion effect for checkerboard and face stimuli (Civile, Quaglia, et al., 2021). It has been established that anodal tDCS delivered at Fp3 (for 10 min at 1.5 mA intensity) could reduce the inversion effect for normal faces when they are the only stimulus category presented, compared to a sham tDCS group. The reduction of the inversion effect in the anodal group was shown to be mainly due to anodal tDCS affecting performance for upright faces, essentially making recognition worse for these faces than a sham. And, when the same anodal tDCS procedure was applied in circumstances where normal faces were intermixed with Thatcherized faces, the inversion effect for normal faces was increased compared to sham. In this case, performance for upright normal faces was enhanced compared to sham, so tDCS had improved recognition performance (Civile, Cooke, et al., 2020).

The results from Experiments 1a and 1b confirm our main prediction and match the predictions made by our simulation work. The key result from both experiments is that for the first time in the literature we directly demonstrate that Thatcherized faces generalize onto normal faces sufficiently to influence recognition of the normal faces themselves. Hence, Experiment 1a has shown that in the sham condition, Thatcherized faces generalize onto normal faces sufficiently to reduce the inversion effect compared to that found in the sham condition of Experiment 1b where normal faces were presented

with checkerboards. This is the first demonstration we are aware of that shows how the inversion effect for normal faces can be influenced (in this case diminished) simply by the type of stimuli intermixed with them. Based on the MKM perceptual learning account that is at the center of our work, we suggest that this change in the inversion effect is due to generalization from the Thatcherized stimuli onto the normal faces. Future studies looking at the face inversion effect should take into account how the presence of different stimulus types along with normal faces could influence the baseline inversion effect that can be obtained for normal faces. Experiment 1b captures what could be termed the pure inversion effect for normal faces. In this experiment, by using checkerboard stimuli, the number of stimuli and conditions of presentation were unaltered compared to Experiment 1a to allow a valid comparison, and generalization onto the normal faces was minimized to allow us to assess the impact of generalization from the Thatcherized faces to normal ones.

Another important result emerges from comparing the inversion effect for normal faces in the anodal groups in Experiments 1a and 1b. Here we see a significant difference with the inversion effect for normal faces in Experiment 1a being larger than that in Experiment 1b, essentially the reverse of the effect found in the sham groups. This result as well is in line with our simulation work and with previous experimental work (e.g., Civile, Cooke, et al., 2020; Civile, McLaren, & McLaren, 2018). However, we must note at this point that strictly speaking, we were not able to predict this effect. What we were able to predict was a 2×2 interaction such that the effect of tDCS would be to reduce the inversion effect in Experiment 1b and increase it in Experiment 1a. This can lead to the effect seen in the anodal groups here when we compare across experiments as long as the difference in the inversion effects in the sham conditions of these experiments is not too large, but it is the changes in the inversion effect that are the real predictions of the model and that we consider now.

For Experiment 1b, the additional analyses revealed the established replicated finding that anodal tDCS reduces the inversion effect for normal faces presented alone (Civile, McLaren, & McLaren, 2018) or, as in this case, presented with sets of stimuli that do not generalize onto them. Thus, the inversion effect in the anodal group is found to be significantly reduced compared to that found in the sham group. The Bayes factor analysis simply confirmed that this result from Experiment 1b is in line with previous work in the literature (Civile, McLaren, & McLaren, 2018). For Experiment 1a, the additional analyses revealed that despite there being a numerical difference, the inversion effect for normal faces was not significantly enhanced in the anodal group compared to the sham. In Civile, Cooke, et al. (2020), this effect was significant revealing that the anodal tDCS procedure could enhance the inversion effect for normal faces when intermixed with Thatcherized ones. We conducted a Bayes factor analysis aiming to examine if the numerical difference found in Experiment 1a for the inversion effect in the anodal versus sham group was in line with the effects found in Civile, Cooke, et al. (2020) and found some good evidence to support this. The fact that this time in Experiment 1a, anodal tDCS did not significantly increase the inversion effect for normal faces versus that for sham, may suggest that this effect would need a larger sample for its reliable demonstration. Hence, it may be the case that this effect is not as robust as the one found in Experiment 1a (i.e., anodal tDCS reducing the inversion effect vs. sham) which has been found to be significant in every study we have reported in the

literature. Nevertheless, the basic components of the predicted 2×2 interaction are clearly present in our data.

We have been able in this article to provide a more detailed explanation of how adding the Thatcherized faces would affect the inversion effect for normal faces. As we mentioned in the introduction, normal upright faces would be affected because Thatcherized faces contain common features (e.g., eyes and mouth) which are more salient because they are unpredicted, and so they capture more of the learning, and this then generalizes to normal upright faces making recognition harder. In addition, there are unaltered features (e.g., the nose) that are common to all faces that would become more salient due to Thatcherization. All of this will have an impact in enhancing generalization from upright Thatcherized faces to upright normal faces.

Now it is time to consider what tDCS might do when Thatcherized and normal faces are tested in combination. We already know that tDCS reduces the inversion effect in normal faces, by reducing performance on the upright faces (Civile, McLaren, & McLaren, 2018; Civile, McLaren, et al., 2020, 2021; Civile, Quaglia, et al., 2021; Civile, Waguri, et al., 2020). We explain this as a loss of error-driven modulation of salience, which makes the common features as or more salient than the unique features, and so reduces discrimination between upright faces. Normally we would expect a reduction in the inversion effect, but in this case, we will have lost the harmful generalization from the Thatcherized faces to a large extent, and this will tend to increase performance on upright normal faces and enhance the inversion effect.

The basic analysis for upright Thatcherized faces is that the eyes and mouth stand out (i.e., are super-salient) because they, in the context of the rest of the face, result in expectations as to what they should look like, and these expectations are not met. The predicted features are not there, and instead have been replaced by other features caused by inversion. This gives them a greater salience than for novel features, as the error is even higher because the predictions are not simply absent, but in some cases wrong. This means that the modulation of salience will be extremely strong, explaining why these features are super-salient. This is not the case after inversion, because then the predictions made are relatively weak, as individuals have little or no experience with inverted faces. This effect is responsible, in part, for the impact that Thatcherized faces have when seen in their upright orientation. Contrast this with normal faces, where many of the features are to some extent predicted, which lowers their salience, and allows the unique features of the face, which are not predicted unless that face is familiar, to be relatively salient, aiding discrimination. But how does all this affect generalization?

When there is a mixture of normal and Thatcherized faces, tDCS decreases the generalization from the latter to the former. This is because the manipulated features in a Thatcherized face will now be very weakly represented instead of super-salient. The result is that normal upright faces benefit from the reduced generalization from the Thatcherized faces consequent on stimulation, and this outweighs the effect that would otherwise be observed due to the reduction in the relative salience of the unique features of the normal faces. Thus, the net outcome is an increased inversion effect for normal faces as confirmed by the behavioral results in our study.

The results in this article also confirm the predictions made by the MKM model. Using a very simple version of the model employing error-based modulation of salience, we have been able to show that our use of the theory can be backed up by simulation, and then have

gone on to confirm those simulation results. In some ways, this is a surprising outcome, as we deliberately did not set out to construct a plausible model of recognition memory, but instead wanted to demonstrate how the principles embodied in the McLaren et al. (1989) theory would lead to the analyses we have offered in previous papers. We believe we have done that, our surprise stems from the fact that the simplistic approach adopted to recognition here cannot be correct. Given this, why are our results so in line with the simulations we offered earlier?

One possible answer is that in reality, the face recognition experiments run in this article permit a much simpler approach to learning and memory than we have previously acknowledged. Our simulations basically amount to casting the task in a very familiar form: a succession of stimuli are associated with an outcome, and then we assess the ability of the network to discriminate the novel S− from all the S+ that have been trained. And note that the network uses distributed representations in a single layer of weights and as such makes no attempt to keep representations of individual stimuli separate, but instead blurs them (and the learning they are involved in) together. This is why this is in no way a plausible model of memory, but our results do suggest that it may be enough to account for performance on this task under these conditions. Anecdotally, participants in this task often report that they had no real recollection of the studied stimuli and felt they were more or less guessing based on some feeling of familiarity with the stimulus in front of them (a view that is particularly prevalent when the stimuli are checkerboards). We speculate that this may simply be our participants reporting the use of something akin to the type of trace strength approach taken here.

In conclusion, in this article we have advanced our understanding of the effects of modulating perceptual learning as indexed by the face inversion effect. In Experiments 1a and 1b we demonstrated that simply presenting normal faces intermixed with Thatcherized ones leads to a significantly reduced inversion effect for normal faces as suggested by our simulations work. This is the first evidence in the literature revealing how the type of stimuli that we present with faces may influence the recognition of normal faces. Importantly, by intermixing normal faces with checkerboards we also established the size of the inversion effect when no harmful generalization is affecting normal faces. In the anodal tDCS groups, our results reveal the shift in the effects that the same tDCS procedure induces depending on the stimuli that normal faces have been intermixed with. The additional analyses looking at the results within Experiment 1a provide some evidence in support of the tDCS procedure increasing the inversion effect for normal faces when intermixed with Thatcherized faces. The additional analyses from Experiment 1b confirmed that in situations where normal faces are presented intermixed with stimuli that do not generalize onto them, anodal tDCS reduces the inversion effect for normal faces. Overall, our results contribute to the perceptual learning and face recognition literature and support the MKM model of these phenomena by revealing how specific manipulated stimuli and a specific tDCS procedure can modulate perceptual learning by either decreasing or increasing the face inversion effect.

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