Causal evidence of the involvement of the right occipital face area in face-identity acquisition

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Abstract

There is growing evidence that the occipital face area (OFA), originally thought to be involved in the construction of a low-level representation of the physical features of a face, is also taking part in higher-level face processing. To test whether the OFA is causally involved in the learning of novel face identities, we have used transcranial magnetic stimulation (TMS) together with a sequential sorting – face matching paradigm (Andrews et al. 2015). First, participants sorted images of two unknown persons during the initial learning phase while either their right OFA or the Vertex was stimulated using TMS. In the subsequent test phase, we measured the participants' face matching performance for novel images of the previously trained identities and for two novel identities. We found that face-matching performance accuracy was higher for the trained as compared to the novel identities in the vertex control group, suggesting that the sorting task led to incidental learning of the identities involved. However, no such difference was observed between trained and novel identities in the rOFA stimulation group. Our results support the hypothesis that the role of the rOFA is not limited to the processing of low-level physical features, but it has a significant causal role in face identity encoding and in the formation of identity-specific memory-traces.

Keywords: identity; face recognition; face perception; occipital face area; transcranial magnetic stimulation;

Introduction

The occipital face area (OFA) is part of the core network of face-selective brain areas, along with the fusiform face area (FFA) and the superior temporal sulcus (STS), and is considered to be involved in early, low-level processing of the physical features of a face (Haxby et al. 2000; Pitcher et al. 2011). In this model of face perception, the OFA creates an initial structural representation based on local attributes, which is subsequently processed holistically by later, higher-level regions in a feed-forward manner.

The notion that FFA, and not OFA represents faces in a holistic manner is supported by imaging studies on healthy participants. Rothstein et al. (2005) have shown that there is a release from adaptation in the OFA when the physical appearance of a face is varied, even when that change comes without the participants perceiving the stimulus as a different identity. Furthermore, in a composite-face illusion experiment Schiltz et al. (2010) observed a release from adaptation in the OFA only when both the bottom and top halves were different, in contrast to the FFA, where changing one or both parts reduced the susceptibility to fMRI adaptation similarly.

Providing direct support for early face-part processing in the rOFA, Pitcher et al. (2007) found that repetitive transcranial magnetic stimulation (rTMS) of the rOFA 60-100 ms after stimulus onset disrupted the discrimination of face parts but did not affect the discrimination of spacing between these parts. However, evidence for a holistic processing taking place in the rOFA comes from a TMS experiment using Mooney faces and objects, where on-line TMS to the rOFA impaired categorization, albeit this effect was not restricted to face stimuli (Bona et al. 2016).

On the other hand, neuropsychological observations strongly suggest that an intact OFA is necessary for the identity-dependent processing of faces and that its impairment maybe also result in symptoms of prosopagnosia (Rossion et al. 2003; Bouvier and Engel 2006). It has been reported that in the absence of contribution from the rOFA, the rFFA does not discriminate individual faces properly (Schiltz et al. 2006;

Dricot et al. 2008). Recent experiments found that intracranial electrical stimulation of the rOFA as well as the rFFA elicits transient effects similar to symptoms of prosopagnosia, including impairments in face matching and recognition, as well as perceived distortions of the face stimulus (Jonas et al. 2012, 2014).

Neuroimaging evidence supporting identity processing in the OFA also exists. In an fMRI adaptation study Xu and Biederman (2010) found that in both the FFA and the OFA, changes of identity produced the largest release from adaptation, and while FFA was also sensitive to changes of expression, the OFA responded only to changes in identity. In a perceptual learning task Vilsten and Mundy (2014) measured, using fMRI, the activity of three face-selective regions (FFA, OFA and STS) in the short breaks between the four blocks of a same-different task involving faces. The authors reported that inter-block activity in all of the three regions correlated with task performance in subsequent blocks, with the level OFA correspondence dropping with each block, while FFA and STS correlations were unchanged. Evidence against a strictly feed-forward flow of information from the OFA to higher-level areas comes from studies demonstrating that these higher-level regions, such as the rFFA, can also be activated in the absence of input from the rOFA due to brain damage (Rossion et al. 2003; Steeves et al. 2006; Rossion 2008). This suggests that the OFA is not necessarily merely an entry point of the face perception network. Based on this evidence, feedback interactions are proposed between the rFFA to the rOFA for establishing a full individual face percept (Fairhall and Ishai 2007; Rossion 2008).

Although recent findings have led to the re-evaluation of the serial, cascade-like model of the neural framework for face processing (Duchaine and Yovel 2015), previous OFA-TMS studies found no on-line effects on identity processing (Pitcher et al. 2007; Gilaie-Dotan et al. 2010). Therefore, the direct, causal evidence for the processing of identity-level information in the rOFA is yet to be provided in healthy participants.

In the current study, we focused on the effects of TMS of the rOFA in the development of familiarity of previously unknown faces using sets of highly variable images (Andrews et al, 2015). We argue that if

identity-specific information is processed in the rOFA, then this information can be utilized to construct image-independent representations of a given identity. Therefore, interfering with the activity of the rOFA during the learning new identities should prevent the formation of such identity-specific memory traces.

The development of representations of unfamiliar identities may arise rapidly, through experience of within-person variability (Jenkins et al. 2011; Burton 2013). Face matching paradigms have been shown to be sensitive measures of familiarity, thereby tracking identity acquisition (Clutterbuck and Johnston 2002, 2005). Clutterbuck and Johnston (2005) have demonstrated that the brief presentations of many different images of the face of a given person is more efficient in producing familiarity than longer exposures to fewer images. In a recent study, Andrews et al. (2015) trained their participants by instructing them to perform an identity sorting task on face-photographs of unknown identities. In a subsequent face-matching task, the participants had to make same-different judgments about pairs of photographs, where previously unseen photos of the two identities presented during sorting, or photos of two novel identities were paired with an image from the same category, or with unrelated foil photographs. The authors found that novel photographs of identities previously encountered during the sorting phase were matched more accurately during the later test phase, indicating that exposure to multiple images of a hitherto unknown identity facilitates the formation of a representation by promoting the extraction of stable, identity-specific information that can be used to recognize new, previously unseen images.

In the current experiment, we have set out to test whether the rOFA is causally involved in the acquisition of such image-independent identity information using fMRI guided TMS. We have used the identity-sorting – face-matching paradigm adapted from Andrews et al. (2015), combined with on-line transcranial magnetic stimulation during the training phase. To adapt the paradigm for use in combination with on-line TMS, instead of a card-sorting test where all images are visible simultaneously

during the task, we have created a computer-based version and developed a sequential sorting procedure where the photographs are presented serially, requiring the participants to sort them into two identities. During this training phase, TMS pulses were applied to the rOFA. In a subsequent face-matching task (Andrews et al. 2015), contrasting performance for the two trained against two novel identities were used to assess image-invariant identity information acquisition. Additionally, two control groups were also assessed: one group received TMS over the vertex during the sorting phase to control for the site-specificity of the stimulation, while the other group performed only the face-matching task, i.e. received no prior training, in order to establish a baseline to which performance in the two TMS groups can be compared.

We reasoned that if rOFA indeed takes part in image-independent memory formation for faces, the disruption of the ongoing processes during the acquisition phase will impair performance in the subsequent test phase.

Methods

Participants

Forty-two participants (21 in both TMS experimental groups, 5 male, mean age, SD: 22.40 ± 4.14) took part in the experiment. A further 17 volunteers (8 male, mean age, SD: 21.52 ± 3.22) participated in the control condition where only the face-matching task was performed, without prior training and TMS stimulation (No Sorting/No TMS group). All of the participants were right handed, their visual acuities were normal or corrected to normal. None of the participants reported previous history of neurological or psychological disorders, drug or alcohol abuse, had no metal implants and were not taking regular medication. Written informed consent was acquired from all participants. All participants tolerated the experimental procedures, and none withdrew because of discomfort with TMS stimulation. All participants were students of the University of Jena, and participated in exchange for partial course

credits or monetary compensation. The experiment was conducted in accordance with the guidelines of

the Declaration of Helsinki, and with the approval of the ethics committee of the University of Jena.
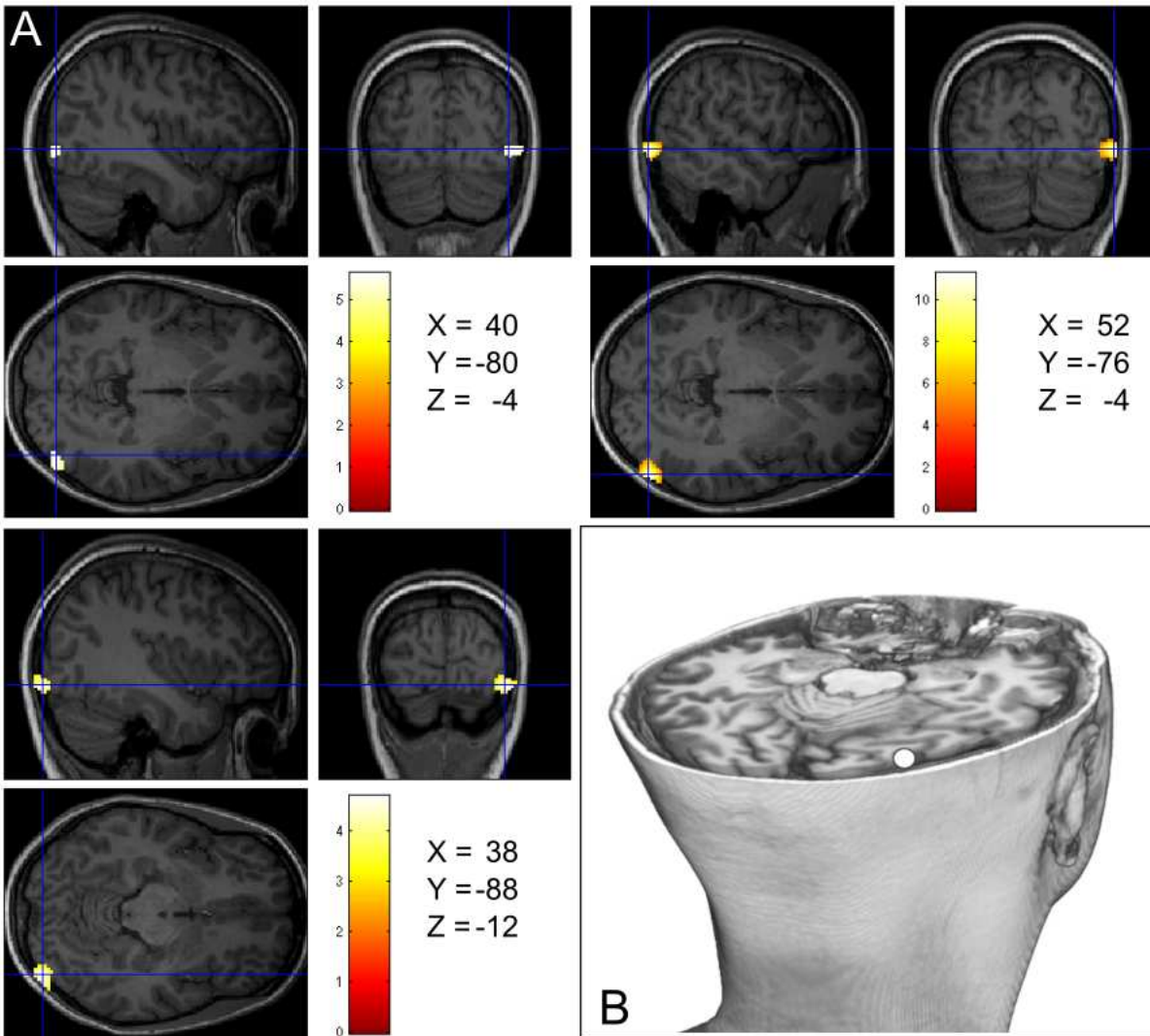
rOFA localization and Neuronavigation-aided TMS

Figure 1. Neuronavigation. (A) The location of the right OFA in three participants with MNI coordinates. (B) TMS neuronavigation site in one representative participant. For details on the anatomical and functional MRI acquisition and neuronavigation, see Methods.

Structural and functional MRI Scanning was performed in a 3T MRI scanner (Siemens MAGNETOM

Prisma fit, Erlangen, Germany) at the Institute for Diagnostic and Interventional Radiology, University of

Jena. High-resolution sagittal T1-weighted images for the 3D head and brain meshes were acquired using

a magnetization EPI sequence (MP-RAGE; TR = 2300 ms; TE = 3.03 ms; 1 mm isotropic voxel size). Functional MRI was acquired with a Siemens 20-channel phased array head-coil and a gradient-echo EPI sequence (35 slices, 10° tilted relative to axial, T2* weighted EPI sequence, TR = 2000 ms; TE = 30 ms; flip angle = 90°; 64 × 64 matrices; 3 mm isotropic voxel size). The right OFA was individually identified in all participants using a standard localizer run which was previously described in Amado et al. (2016), Briefly, 20 s epochs of faces, objects and Fourier-randomized images of faces were interleaved with 10 s of blank periods. None of the face images presented during the localizer were included in stimulus set of the TMS experiment. Forty stimuli were presented within each block. Each stimulus was shown for 300 ms and was followed by a 200 ms blank period (corresponding to a stimulation frequency of 2 Hz). Pre-processing and statistical analysis were conducted as described in Cziraki et al. (Cziraki et al. 2010). The right OFA was selected individually on the single subject level from the thresholded ($p<0.001_{uncorrected}$) t-maps of the contrast faces vs. Fourier-randomized faces and objects. Mean MNI coordinates (±SE) for the right OFA (n=21) were x = 42.64 (1.17), y = -78.05 (1.44), z = -8.47 (0.99), (**Figure 1**).

The individual rOFA coordinates were used for individualized Neuronavigation-aided TMS. Neuronavigation was carried out using a PowerMag View (MES Medizintechnik GmbH) Neuronavigation system. TMS stimulation was delivered at 65% maximum stimulator output, using a PowerMag 100 Research Stimulator (MES Forschungssysteme GmbH).

Experimental procedure

Stimulus presentation

Stimuli were based on Andrews et al., 2015 and 2016, acquired using an internet image search engine. Images of Training and Novel identities were ambient (Jenkins et al. 2011; Sutherland et al. 2013), grayscale photographs of Dutch celebrities unfamiliar to our German participants (training: Chantal Janzen (CJ) and Bridget Maasland (BM), novel: Gigi Ravelli (GR) and Tatjana Simic (TS)). Foil images were of faces of 60 persons with similar age and hair color to the four target identities. Of concern was in

these previous investigations, as in our own, that the appearance of the depicted identities should vary naturally, as a result of both environmental circumstances (such as lighting, camera parameters and view angle) and within-person variation (e.g. hair style, facial expression, etc.). Therefore, no further processing was performed on the images. As potential prior familiarity with our stimulus material could affect the results of the matching task, unfamiliarity with the stimulus faces was confirmed for each participant after the experiment.[1] Stimuli were 6.23° × 8.54° visual angle in size, and were presented on a uniform gray background on a BenQ LED display at 1680 × 1050 pixel resolution with a refresh rate of 60 Hz and a viewing distance of 60 cm. The experimental program was written in PsychoPy (Peirce 2007).
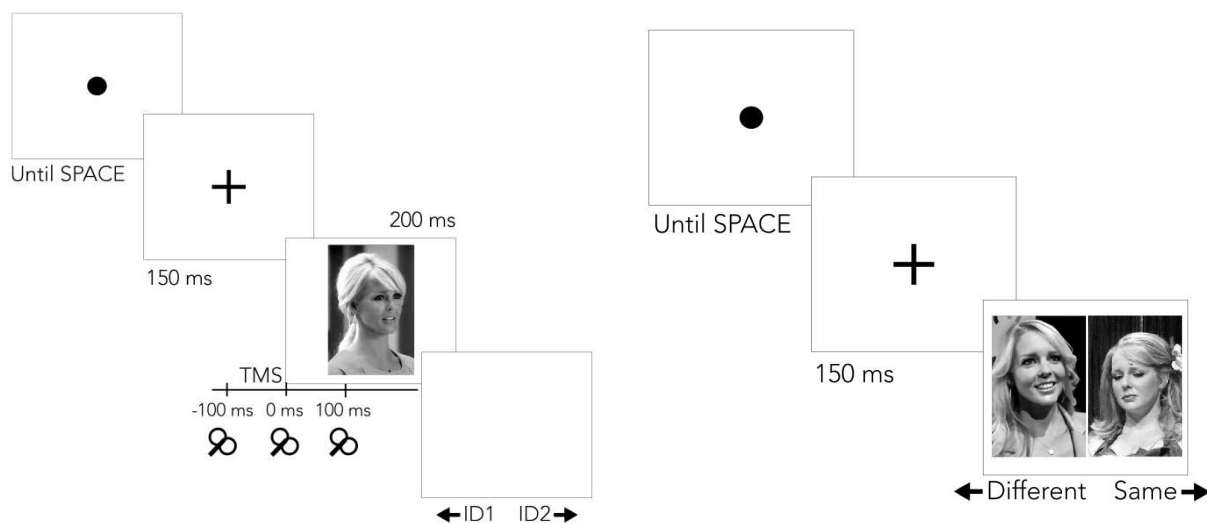

Figure 2. Experimental procedure. (A) Sequential sorting task. Participants sorted sixty photographs of two previously unknown identities (30 photograph each). TMS was applied 100 ms before, with the onset of, and 100 ms after the stimulus onset. Each stimulus was presented for 200 ms. (B) Face matching test. In each trial the participants saw two photographs, and had to indicate whether they depicted the same person, or two different persons.[2]

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[1] A single participant indicated a sense of familiarity with some of the face, but was unable to provide further, specific details. Data from this participant was excluded from the analysis.
[2] All images in **Figure 1** are of identity CJ. *Left* and *middle*: By AVROTROS (https://www.youtube.com/watch?v=UOXfiNY-lYQ) [CC BY 3.0 (http://creativecommons.org/licenses/by/3.0)], via Wikimedia Commons. *Right*: By Sebastiaan Beens (Wikiportrait) [CC BY 3.0 (http://creativecommons.org/licenses/by/3.0) or GFDL (http://www.gnu.org/copyleft/fdl.html)], via Wikimedia Commons. These pictures were not part of the actual stimulus set.

Learning phase – Sequential sorting

Participants were instructed to sort 60 photographs (30 of CJ and 30 of BM), presented sequentially and in a randomized order, into two identities, using the left and right buttons of a computer keyboard. At the beginning of the experiment participants were told that they will see several images of two identities and their task is to sort them into two groups by pressing one button for one person and another one for the other person. Participants were also told that they could choose the assignment of identities to the left or right button, but the same assignment must be applied consistently throughout the task. With a fixation point presented at the center of the screen, the participants self-initiated each trial by pressing the space bar. Then a fixation cross was presented for 150 ms, followed by the images. TMS impulses were applied either to the rOFA or to the Vertex, depending on the experimental group, 100 ms before, concurrent with, and 100 ms after stimulus onset (**Figure 2A.**). The volunteers received no feedback on their performance during the execution of the task.

Test phase – Face matching

The subsequent face-matching task was a computerized version of the paradigm described in Andrews et al. (2015). The participants were instructed to indicate whether two photographs, presented side-by-side horizontally on the screen (size: 6.23° × 8.54°, closest edge 1.34° from the center), were of the same person or depict two different identities, using the left (for different) and right (for same) arrow buttons (**Figure 2B.**). One hundred and twenty matching trials were completed in total. These were 15 same-ID and 15 different-ID trials for BM and CJ (trained, sorting-task identities), and 15 same-ID and 15 different-ID trials for GR and TS (novel identities). The presentation order was randomized independently for each participant. The third, control group took part only in this face-matching task. Again, no on-line feedback regarding matching accuracy was provided to the participants.

To test the effects of on-line TMS during the sorting task between the two TMS stimulation groups, accuracies and reaction times were analyzed using one-way ANOVAs with stimulation Group (rOFA,

Vertex) as the between-subject factor. To assess the success of identity learning, reaction times and hit rates in the subsequent face-matching test were entered into a 3 (Group: rOFA, Vertex, No Sorting/No TMS) × 2 (Stimulus type: Novel IDs, Trained IDs) repeated measures ANOVA. Furthermore, an index of identity learning was calculated by subtracting the hit rates for novel identities from those for the trained identities in each participant. This index was analyzed using a one-way ANOVA with experimental Group (rOFA, Vertex, No Soring/No TMS) as between-subject factor. Significant main effects and interactions were followed up by Fisher's LSD tests. All analyses were two tailed and were conducted with a significance level of $p < 0.05$.

Results

Sorting phase

As indicated by a One-Way ANOVA on hit rates, ($F_{1, 40} = 0.51$, $p = 0.47$, $\eta_p^2 = 0.012$), the sorting performance of the two TMS stimulation groups did not differ significantly (Vertex mean 64.68 ± SD: ± 12.14%, OFA: 67.38 ± 12.21%). Furthermore, there was no difference in reaction times between the two stimulation groups either ($F_{1, 40} = 1.82$, $p = 0.18$, $\eta_p^2 = 0.04$; Vertex: 1.01 ± 0.36 s, rOFA: 0.88 ± 0.21 s).

Matching phase

The analysis of the matching task accuracies showed no statistically significant main effect of stimulation Group ($F_{2, 56} = 1.66$, $p = 0.20$, $\eta_p^2 = 0.06$), while the main effect of Stimulus Type was significant ($F_{1, 56} = 7.51$, $p = 0.008$, $\eta_p^2 = 0.09$). Most importantly, the significant interaction between the two factors ($F_{2, 56} = 5.67$, $p = 0.006$, $\eta_p^2 = 0.18$, **Figure 3A**) and the Fishers' LSD post-hoc tests suggest that the performance for Trained IDs differ significantly from that of Novel IDs in the Vertex control group ($p = 0.006$), while no such difference was observed in the rOFA ($p = 0.82$) and in the No Sorting/No TMS control groups ($p = 0.93$). Accuracies for Training IDs did not differ between the rOFA and Vertex control groups ($p = 0.29$), and there was no significant difference between accuracies for the Novel IDs either ($p = 0.12$). Also, we

observed no significant difference between the No Sorting/No TMS and the rOFA group regarding accuracies for Training (p = 0.11) or Novel (p = 0.14) identities, while the difference in Training ID matching accuracy was significantly different between the No Sorting/No TMS and the Vertex groups (p = 0.011).

To quantify the effect of sorting, for each participant we subtracted the accuracies for Novel IDs from those for Trained IDs. The analysis of the accuracy differences in the three groups further corroborate our findings ($F_{2, 56}$ = 5.67, p = 0.006, η^2_p = 0.17; **Figure 3B.**), as the Fishers' LSD post-hoc test showed no difference between the rOFA and the No Sorting/No TMS groups (p = 0.90), while both of these groups differed significantly from the vertex group (rOFA: p = 0.005, No Sorting/No TMS: p = 0.006).

The analysis of the reaction times showed no main effect of Group ($F_{2, 56}$ = 1.44, p = 0.245, η^2_p = 0.05) or Stimulus type ($F_{1, 56}$ = 3.53, p = 0.055, η^2_p = 0.06), nor an interaction of the two factors ($F_{2, 56}$ = 0.68, p = 0.50, η^2_p = 0.02).
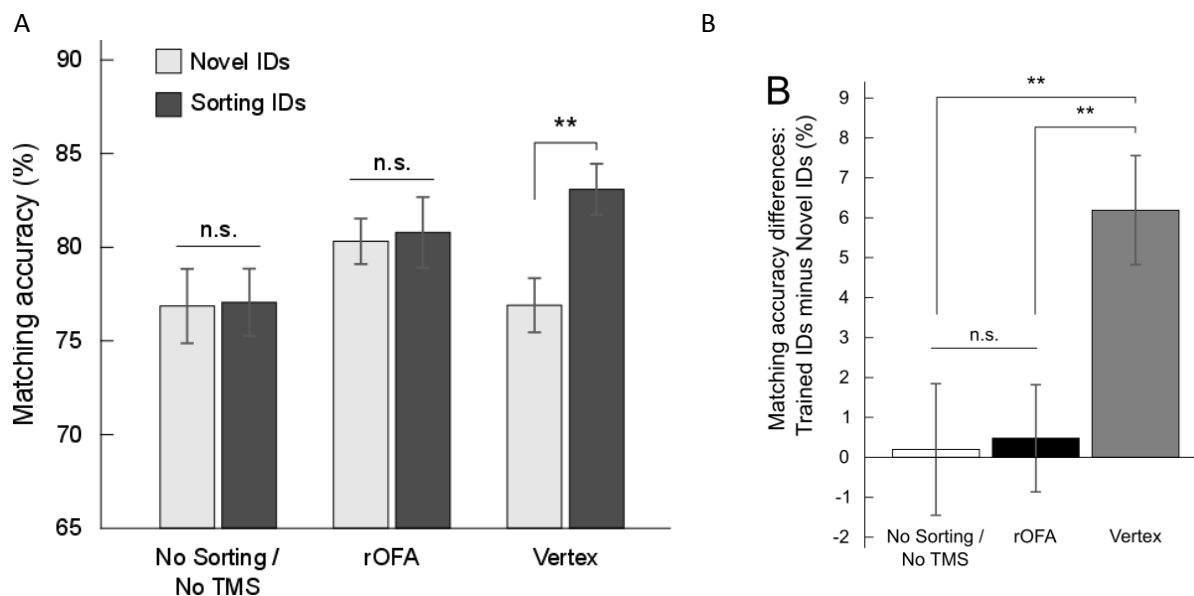

Figure 3. Accuracies in the face-matching task. **A)** A learning effect was observable in the Vertex control condition, indicated by the difference between accuracies for Training and Novel identities (n = 21, p = 0.006). This effect was missing in the rOFA stimulation group (n = 21, p = 0.82) and in the No Sorting/No TMS group (n = 17, p = 0.93). **B)** Differences in matching accuracies between Training and Novel identities in the three experimental groups. No difference between the rOFA and the No Sorting/No TMS groups was found (p = 0.90), while both of these groups differed from the Vertex TMS group (rOFA: p = 0.005, No Sorting/No TMS: p = 0.006). Error bars denote SEM.

Discussion

There is a profound difference between how the brain processes familiar and unfamiliar faces (Hancock et al. 2000). While familiar faces are recognized with ease and high accuracy (Burton et al. 1999), matching two unfamiliar faces is surprisingly hard (Burton et al. 2011; White et al. 2014). In order to identify familiar faces, general and stable, image-independent representations need to exist. These representations should allow for transient within-person variabilities, due to e.g. changes of hair-style, make-up, mood and ageing, but they also should remain sensitive to the invariable characteristics of faces that enables one to differentiate between different identities (Andrews et al. 2015, 2016). Such representations develop over time, via multiple encounters with a given person, whereby a transition from relying largely on pictorial codes, to relying on structural codes occurs (Burton et al. 2011). Despite the progress in uncovering the cognitive framework, the neural substrate of this process is still far from being fully understood.

In the current study we have investigated the role of the rOFA in the formation of facial identity information by applying TMS during a sequential sorting task in the acquisition phase, and measuring the performance advantage for the sorted identities against novel identities. We found that while no differences were present in sorting performance, the significant learning effect present in the Vertex stimulation group could not be observed in the rOFA stimulation group.

No on-line effect of TMS on sorting performance

The lack of difference in sorting performance between the two TMS stimulation groups is in line with results from previous studies that had found no effects of on-line TMS on identity matching itself (Pitcher et al. 2008; Gilaie-Dotan et al. 2010). In a matching task where participants had to make same-different decisions about the identities or facial expressions of sequentially presented face-pairs, Pitcher et al. (2008) found no effect of on-line TMS to the rOFA concurrent with the test stimulus on identity matching, using stimuli from Ekman and Friesen's (1976) facial affect series. In an identity discrimination

task, in which participants were instructed to determine whether two successively presented photographs of famous persons depicted the same or different individuals, Gilaie-Dotan et al. (2010) found no effect of rOFA TMS applied during the interstimulus interval between the presentation of the face pairs. The authors of these studies interpreted their findings as a lack of evidence for identity-selectivity in the rOFA. If rOFA represents identity-level information, why did on-line stimulation of the rOFA have no effect on the sorting-task performance itself in our study and in previous TMS experiments investigating identity-matching performance? It can be suggested that, similarly to the sorting task of the current study, in the delayed match-to-sample task of Pitcher et al. (2008) the same-different decisions were conducted on a trial-by trial basis. Therefore, it can be interpreted as a simple perceptual matching process, which is presumably not affected by the disruptive effects of rOFA stimulation. Furthermore, the accumulation of identity-specific information was not tested in either of these previous studies. The same reasoning applies to the study by Gilaie-Dotan et al. (2010), with the addition that their stimuli were images of identities the participants were already pre-experimentally familiar with, thus had already developed representations for them. Our study, however, explicitly tested the success of the experimental formation of familiarity for previously unknown identities via combining several images of the same person into a stable representation, resembling real-life face learning situations.

Reduction of the effect of training after TMS of the rOFA

Strikingly, TMS stimulation of the rOFA abolished the advantage of the sorting phase on face-matching accuracy entirely in the subsequent matching task: the difference in matching performance for novel and trained IDs was as similar in the rOFA TMS stimulation group to that of the no-training group. This suggests that the disruption of the rOFA functions during identity acquisition from multiple instances impairs the formation of identity-dependent memory traces resulting from the abstraction of image-invariant information. Of course, this leaves open the major question: what actually is this image-invariant information? This is a very difficult issue, and one which is of interest to all those concerned

with face recognition - from engineering to neuroscience. While this must form the basis for future research, the characteristics of the OFA within the face perception network do provide some clues.

Based on empirical evidence from TMS-fMRI (Pitcher et al. 2014) and non-human primate-fMRI (Fisher and Freiwald 2015) investigations, a functional dorsal/ventral split in face-selective areas has been proposed (Duchaine and Yovel 2015). The dorsal stream (the posterior superior temporal sulcus face area, the anterior superior temporal sulcus face area, and the inferior frontal gyrus face area) specializes on the processing of dynamic information from faces. The ventral stream (OFA, FFA, and the anterior temporal lobe face areas) extracts form information, i.e. structure and surface properties from faces, represents invariant features such as identity, sex, and age, and contributes to the recognition of facial expressions as well. The flow of information between the primary visual areas and higher regions, as well as the connections among the higher regions, is not strictly serial and hierarchical. Parallel connections exist between the primary visual areas and both the OFA and the FFA (Gschwind et al. 2012; Pyles et al. 2013) and there is also evidence of feedback connections between the FFA and the OFA as well (Steeves et al. 2006). Lesion studies show that without an intact rOFA, the rFFA fails at the proper discrimination of individual faces (Dricot et al. 2008; Rossion 2008). Thus, an integrated representation of an individual face is the result of the interplay between the FFA, providing a general face template, and the OFA, performing a finer-grained perceptual analysis, via a reentrant circuitry (Rossion 2008).

Previous investigations have shown that the OFA takes part in the processing of visual stimuli in a variety of ways. Some of these functions appear to be low-level, holistic, and not restricted to face stimuli. For example, the rOFA has been shown to be involved in the detection of symmetry, both in low-level dot configurations, and in faces (Bona et al. 2015). Similarly, holistic stimulus categorization was shown to be impaired by TMS to the rOFA, irrespective of stimulus type (Bona et al. 2016). Also, early-onset (40-50 ms) TMS to the rOFA (and EBA) impaired performance for both preferred and non-preferred categories (faces and bodies) in a delayed match-to-sample task (Pitcher et al. 2012). On the other hand, a recent

fMRI study (Henriksson et al. 2015; van den Hurk et al. 2015) showed evidence of a specialized, faciotopic organization (i.e. the distances between cortical locations with preference for facial features also reflecting the topology of these features in a face) in the OFA (and to a lesser extent in the FFA as well). Furthermore, task demands have also been demonstrated to influence the population receptive fields in the IOG, with attention actively enhancing spatial representations in the ventral visual pathway (Kay et al. 2015). These characteristics might constrain the type of visual information which drives the type of face learning we have reported here.

Limitations

It is worth to note that while the rOFA TMS eliminated the advantage of Sorting over Novel stimuli, there was no statistical difference in the raw performance for the trained stimuli between the rOFA and Vertex TMS groups. The lack of this effect might be linked to differences in baseline performance due to the vast inter-individual differences in face recognition (Wilmer et al. 2010; Zhu et al. 2010; Yovel et al. 2014). This, however, is unlikely as the Novel stimuli were neither different between rOFA and Vertex TMS groups.

Finally, a general methodological constraint of virtual-lesion TMS technique is that the effects of stimulation may propagate through connected brain regions (Ruff et al. 2009), rendering the interpretation of TMS experiments more challenging. Further investigations are needed to specify the overall network-effects of TMS on connected brain regions (Parreira et al. 2016).

Summary

In summary, we have shown that disrupting the functions of the rOFA by TMS during a training phase abolishes identity information acquisition, thereby, for the first time we have demonstrated that the rOFA plays a causal role in the formation of image-independent representations for facial identities. These findings indicate that the rOFA is involved in identity learning from multiple instances and in the creation of identity-dependent memory traces. This result questions the simple hierarchical model of

face processing and suggests the causal role of the OFA in higher-level processing steps, as well as the global processing of human faces in the occipito-temporal cortex.

Acknowledgements

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