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

Géza Gergely Ambrus[a,*], Fabienne Windel[a], A. Mike Burton[c], Gyula Kovács[a,b]

[a] Institute of Psychology, Friedrich Schiller University Jena, 07743 Jena, Germany
[b] Person Perception Research Unit, Friedrich Schiller University Jena, 07743 Jena, Germany
[c] Department of Psychology, University of York, UK

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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.

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. Rotshtein 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).

* Correspondence to: Institute of Psychology, Friedrich Schiller University Jena, Leutragraben 1, 07743 Jena, Germany.
E-mail address: geza.ambrus@uni-jena.de (G.G. Ambrus).

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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

Structural and functional MRI Scanning was performed in a 3 T 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. (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), (Fig. 1).

The individual rOFA coordinates were used for individualized