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ORIGINAL ARTICLE

TMS of the occipital face area modulates cross-domain identity priming

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Abstract
Accumulating evidence suggests that besides its function in early facial feature processing, the role of the right occipital face area (rOFA) extends to higher level, image-independent processing. Recent studies hint at the possibility that the activity of this region can be modulated by semantic information as well. To test whether the OFA is sensitive to semantic information in a functionally relevant way, we implemented a cross-domain, name-face priming paradigm combined with state-dependent transcranial magnetic stimulation, whereby stimulation preferentially facilitates the processing of attributes encoded by less active neural populations. Our volunteers performed a familiarity decision task for target face images preceded by primes that were either the name of the same identity (congruent), a name of a different person (incongruent), or the character string 'XXXXX' (no prime). Stimulating the rOFA at target stimulus onset, we observed the disappearance of the behavioral disadvantage of incongruent primes, compared to the vertex control condition. Performance in the congruent and no prime conditions remained intact. This result suggests the existence of neural populations in the rOFA that take part in the semantic processing of identity, probably in interplay with other nodes in the extended face network.

Keywords Transcranial magnetic stimulation · Face perception · Priming · Familiarity · Occipital face area

Introduction

The occipital face area (OFA, Gauthier et al. 1999) has previously been described as an early face-selective region that encodes dominantly low-level stimulus features of a perceived face (Rotshtein et al. 2005; Pitcher et al. 2008; Guntupallia et al. 2016). Accordingly, current theories of face perception suggest that the formation of a coherent face-identity percept occurs in cortical areas located more downstream in the hierarchy, including the fusiform face area, FFA, superior temporal sulcus, STS and the anterior temporal lobe (ATL) (Kriegeskorte et al. 2007; Natu and O'Toole 2011; Weibert and Andrews 2015; Weibert et al. 2016).

However, evidence accumulating from diverse fields, such as neuropsychological observations (Rossion et al. 2003; Bouvier and Engel 2006; Schiltz et al. 2006; Dricot et al. 2008), intracranial electrophysiology (Jonas et al. 2012, 2014, 2015) and functional neuroimaging (Xu and Biederman 2010; Vilsten and Mundy 2014; Engell et al. 2018), suggest that the OFA might not only function as an entry point for the face perception network restricted to early, low-level processing, in the hierarchy of ever-increasing abstraction. Newer models, informed by structural and functional connectivity findings [e.g. (Gschwind et al. 2012; Pyles et al. 2013)] propose synchronized, ongoing processing via re-entrant connections between parts of the face-network to form a representation of facial identity (Pitcher et al. 2014; Rossion 2014; Duchaine and Yovel 2015; Trapp et al. 2018). Such a conclusion gained further support from two recent TMS experiments from our laboratory as well. First, the causal role of the right OFA in face-identity acquisition has been demonstrated, using highly variable, "ambient" images (Burton et al. 2011; Andrews et al. 2015), showing that TMS of the right OFA eliminates the effects of prior training on a face-matching task (Ambrus et al. 2017). Second, in another study TMS eliminated the advantage of

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face–face repetition priming, thereby supporting the role of the OFA in the formation of image-independent representations (Ambrus et al. 2017a, b). Most importantly for the aims of the current study, a recent fMRI study tested the neural activations, applying cross-domain identity priming (Bruce and Valentine 1985; Burton et al. 1998) where the prime was the name of a famous person and the target could either be a congruent (i.e. depicting the same identity) or incongruent face (Amado et al. 2018). A relevant finding of this study regarding the organizational hierarchy of the face perception network was that congruent name primes not only lead to a lower BOLD signal in the bilateral FFA but, surprisingly, also in the bilateral OFA. This cross-domain modulation of the face-evoked fMRI signal by the name primes suggests that the processing of identity information in the OFA is not restricted to images of faces, but is sensitive to semantic information as well.

To further test the cross-domain identity processing in the OFA, we adapted the design by Amado et al. (2018) for use in a state-dependent TMS experiment with a paradigm similar to the one previously used to test image repetition priming (Ambrus et al. 2017a, b). The state-dependency of TMS (Silvanto et al. 2017; Silvanto and Cattaneo 2017) presumes that the effect of stimulation depends on the prior state of the stimulated neurons: TMS typically facilitates the relatively less active or excitable neurons (Silvanto and Pascual-Leone 2008). In a priming paradigm, this leads to the selectively facilitated processing of unprimed stimuli by the TMS pulse, causing a relative improvement in reaction times and/or accuracies compared to the primed stimuli. This state-dependent characteristic of the TMS effect can thus be utilized in investigating if the targeted cortical area contains neuronal populations that are tuned to specific stimulus properties, as the TMS pulse will selectively modulate these.

Here, our hypothesis was that if the right OFA were involved in the cross-domain processing of face identity, priming effects that arise from the neural responsiveness to identity would be impaired by TMS stimulation. In our previous image priming experiment we observed increased performance for different identity prime-target face-pairs when the right OFA was stimulated at target onset, indicating the disruption of identity-specific priming (Ambrus et al. 2017a, b). Here, we tested if this effect extends to visually presented non-face primes, such as the names of familiar celebrities as well.

To this end, our participants performed a familiarity decision task for faces (see Fig. 1), preceded by either the name of the same (Congruent) or of a different (Incongruent), famous individual while single-pulse TMS was delivered at target onset to either the right OFA (rOFA) or to the vertex as control area, in two separate sessions.

In line with our predictions, we observed that TMS of the rOFA increases response accuracy in the incongruent (unprimed) condition, thereby eliminating identity-specific priming. These findings further support the hypothesis that populations of neurons in the right OFA exist that participate in cross-domain processing of identity and argue against the role of the right OFA as a simple “gatekeeper” of face processing.

Materials and methods

Participants

Eighteen healthy German volunteers, students of the University of Jena, participated in the experiment in exchange for partial course credits or monetary compensation. Three participants were excluded due to a low number of remaining trials ($<75\%$) after removing those with falsely categorized stimuli (see below), and one participant dropped out due to discomfort with the TMS stimulation. The final sample thus consisted of 14 participants [2 male; all right-handed, mean age (± SD): 24.06 (2.86) years]. None of the participants reported a previous history of neurological or psychological disorders, drug or alcohol abuse, none had metal implants or were taking regular medication relevant to the study. Written informed consent was obtained from all participants. The experiment had been 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

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 (rOFA) was identified individually by standard fMRI functional localizer runs, described in detail elsewhere (Amado et al. 2018). The location of the rOFA was determined individually, as an area responding more intensely to faces than to objects and Fourier randomized versions of faces ($p < 0.0001_{\text{UNCORRECTED}}$). The average MNI coordinates (± SE) of the rOFA were 42.86 (1.6), − 79.36 (1.68), − 9.3 (1.1).

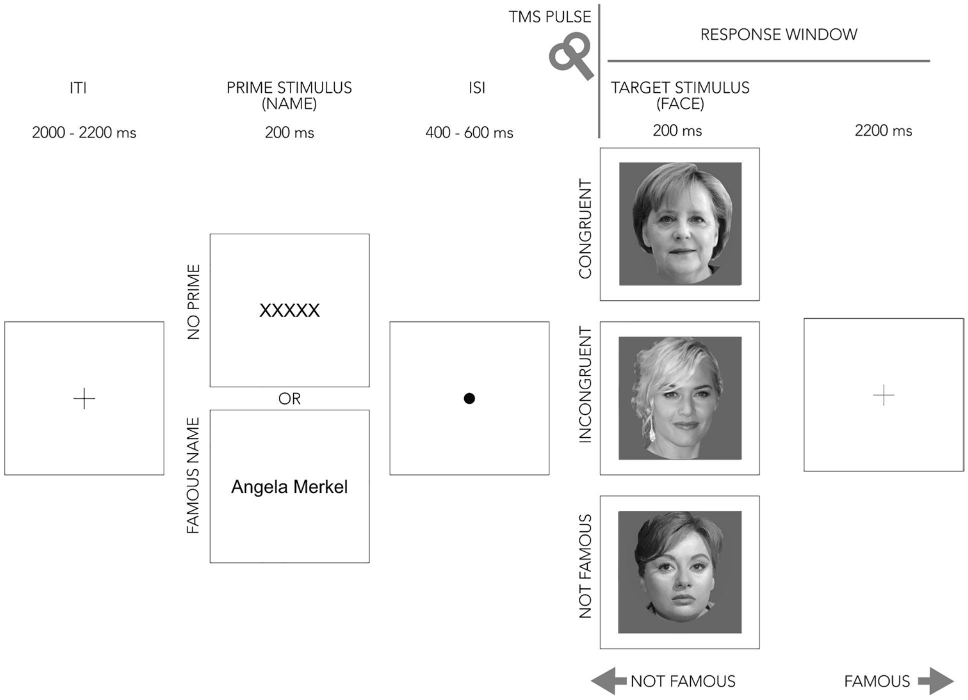

Fig. 1 The cross-domain name-face priming paradigm. A trial began with the presentation of a fixation cross, followed by the presentation of the prime stimulus. This was either the name of a famous person or the character series "XXXXX". Following the presentation of a fixation cross a face congruent with the prime name, a face of another famous person, or an unknown person was displayed (target stimulus). A single TMS pulse was delivered together with the onset of the target stimulus. The participants were instructed to make familiarity judgements (famous/not famous) for the faces. Image credits: Congruent: Armin Linnartz [CC BY-SA 3.0 de (https://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons (Angela Merkel, the current German Chancellor); Incongruent: Georges Biard [CC BY-SA 3.0], via Wikimedia Commons (Kate Winslet, American actress); Not famous: Fortepan/Kotnyek Antal [CC BY-SA 3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons (Hédi Váradi, Hungarian actress). These images were not part of the actual stimulus set

Transcranial magnetic stimulation

TMS was delivered using a PowerMag 100 Research Stimulator (MES Forschungssysteme GmbH). Neuronavigation was performed using a PowerMag View (MES Medizintechnik GmbH) system. All participants took part in two TMS sessions with at least 4 days apart. The order of the stimulation conditions (rOFA, vertex) was counterbalanced across participants. A single, biphasic TMS pulse with 65% maximum stimulator output (Silvanto et al. 2007; Cattaneo et al. 2008, 2009, 2010, 2012; Cattaneo and Silvanto 2008a, b; Renzi et al. 2011; Mattavelli et al. 2011; Perini et al. 2012) was delivered together with the face stimulus onset either to the rOFA or to the vertex. During the TMS procedure, the participants' head was stabilized by a head rest with a viewing distance of 60 cm. The coil handle was pointing upwards. To guarantee that the coil was placed correctly, its position was continuously monitored during the experiment.

Experimental procedure

The experimental procedure was adapted and modified from Ambrus et al. (2017a, b). Two groups of visual stimuli were used: faces as targets and names as prime stimuli. The face stimulus pool included 40 familiar famous and 40 unfamiliar faces. The name stimuli (Arial font with size 26 in black color) corresponded to the first and the last names of the selected familiar faces (for example, Angela Merkel). Thus, in total, 40 familiar names were used in this experiment. The probability of sex was equalized (i.e. 50/50% female/male) for all stimulus groups. The unfamiliar identities were Hungarian celebrities, unknown to our group of German participants. The face stimuli were eye-aligned and converted to greyscale with equal contrast and luminance SHINE toolbox; (Willenbockel et al. 2010) subtending a visual angle of 7.3° in diameter. Stimuli pairs also contained a "non-primed", neutral control condition where the prime was the character-series "XXXX". Names and images were not repeated across sessions, and were randomized across participants. Trials with unfamiliar face identities, necessary for observing priming effects, were considered fillers, and were not further analyzed. Stimuli were presented centrally on a uniform gray background (BenQ LED display, 1680 × 1050 pixel resolution, refresh rate 60 Hz). The experiment was written in Psychopy (Peirce 2009).

In each experimental session, a total of 180 trials were presented. Depending on the trial type, prime and target stimuli were either a famous name and face, representing the same identity (congruent), a famous name and a famous face, of two different famous identities of the same sex (incongruent), a famous name and a non-famous face (not famous), or the character string ‘XXXXX’ and a face (no prime). Each trial began with a fixation cross (200 ms), followed by the prime name (200 ms). Thereafter a fixation point was presented (400–600 ms), which was followed by the target image (present for 200 ms), accompanied by the TMS pulse at stimulus onset. The participants were instructed to perform a two-alternative forced-choice familiarity task for the target face images by pressing the right arrow key when the face was perceived as familiar and the left when it was perceived as unfamiliar (Fig. 1). The prime stimulus required no response. A short practice phase was included at the beginning of each session to familiarize the participants with the task and response mapping. The practice identities were not used in the main experiment. The test consisted of two blocks, with self-paced breaks between them. Trial conditions and durations were intermixed and presented in a random order.

At the end of each session, we verified the participants’ familiarity with the presented faces and names. The participants filled out two digital forms, one presenting the faces, the other the names of the previously seen identities, requiring to identify the familiar ones by naming them or by giving information about their occupation, nationality or any other property of fame. Trials with famous faces or names that were not recognized in this verification phase and trials where non-famous faces were falsely categorized as famous identities were removed from the final statistical analysis. Where the ratio of such excluded trials exceeded 25%, the participant was removed from data analysis ($n = 3$).

Results

Accuracy

We found a main effect of the condition [$F(2, 26) = 10.894$, $p < 0.001$, $\eta_p^2 = 0.456$; depicted in Fig. 2a]. In other words, responses were more accurate in the congruent when compared to the incongruent ($p = 0.001$) and control ($p = 0.032$) conditions. Accuracies in the incongruent and the control trials were not significantly different ($p = 0.251$). There was no main effect of TMS stimulation site [$F(1, 13) = 0.545$, $p = 0.473$, $\eta_p^2 = 0.040$] but we found an interaction between the TMS stimulation site and the condition [$F(2, 26) = 5.279$, $p = 0.012$, $\eta_p^2 = 0.289$; see Fig. 2a]. This interaction was driven by the *Incongruent* condition as the stimulation of the rOFA led to better performance when compared to the vertex ($p = 0.035$). For the other conditions (i.e. congruent

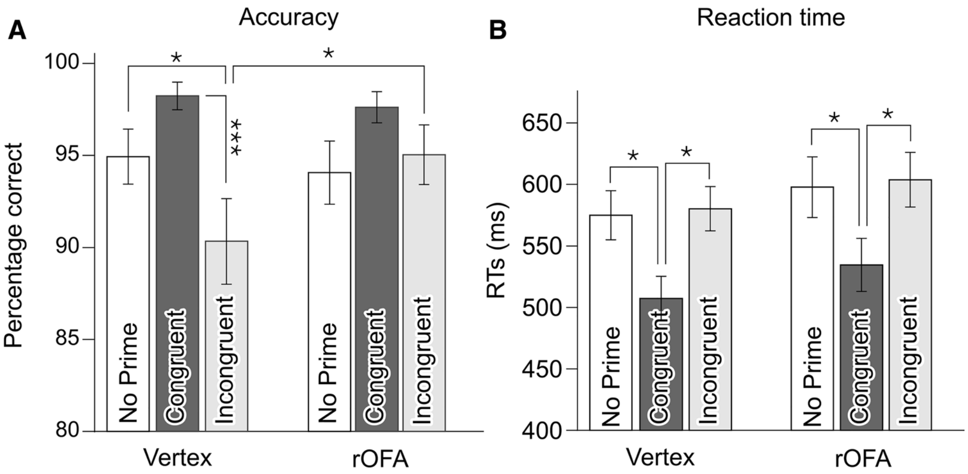

Fig. 2 **a** Accuracies in the rOFA and vertex stimulation conditions for the three trial types. Single pulse TMS of the rOFA at target onset eliminated the performance-reducing effect of an incongruent prime, as evidenced by an increased hit rate ($p = 0.03$) when compared to the control site. **b** Reaction times in the rOFA and vertex stimulation conditions for the three trial types. TMS did not affect reaction times differentially; the priming effect—shorter reaction times for congruent compared to incongruent trials—were observable in both TMS stimulation conditions. Additionally, reaction times in the no-prime control condition were significantly longer than those in the congruent condition. $^{*}p < 0.05$, $^{***}p < 0.001$. Error bars denote standard errors

and control), no significant differences were observed across the stimulation sites (rOFA and Vertex). This suggests that the rOFA plays a causal role in the creation of cross-domain priming effects and that this is manifest in the enhanced performance after rOFA TMS for the incongruent condition.

Reaction times

We found a significant priming effect [main effect of condition; $F(1, 26) = 52.864$, $p < 0.0001$, $\eta_p^2 = 0.803$; depicted in Fig. 2b]; responses were faster in the congruent when compared to the incongruent ($p = 0.001$) and control ($p = 0.002$) trials. No significant difference was detected in the RTs of the *Incongruent* and the control conditions ($p = 0.784$). Furthermore, there was no main effect of TMS stimulation site [$F(1, 13) = 2.791$, $p = 0.120$, $\eta_p^2 = 0.177$) and no interaction between the condition and TMS stimulation site factors [$F(2, 26) = 0.089$, $p = 0.915$, $\eta_p^2 = 0.007$].

Discussion

The major finding of the current experiment is that cross-domain identity priming is affected negatively by the transcranial magnetic stimulation of the right OFA.

Priming effects can be elicited by similar, closely related or associated stimuli (Bruce and Valentine 1985), and the existence of cross-domain priming [i.e. prime and target presented in different modalities, see (Spence 2011)] for names and faces has been previously demonstrated (Schweinberger et al. 2002; Jemel et al. 2005). To explore the neural underpinnings of this phenomenon, a recent study from our laboratory (Amado et al. 2018) looked at fMRI responses in face-selective areas in a name-face priming paradigm. Congruent (i.e. same identity) name-face pairs lead to a lower BOLD signal in bilateral FFA and, surprisingly, also in the OFA. This effect is similar to the fMRI adaptation observed for repeated face stimuli [for a review see (Grill-Spector et al. 2006)]. fMRI signal modulation in the FFA is not entirely unexpected, as this higher-level area has been linked to identity processing in a large number of studies (Kriegstein et al. 2005; Rotshtein et al. 2005; Gilaie-Dotan and Malach 2007; Nestor et al. 2011; Goesaert and Op de Beeck 2013; Verosky et al. 2013; Anzellotti et al. 2014; Axelrod and Yovel 2015; Weibert et al. 2016). Accordingly, recent multivariate pattern analysis studies has found that semantic person-related context information can be decoded from the FFA, suggesting that its processing reaches beyond the analysis of visual features (Van Den Hurk et al. 2011; Ghuman et al. 2014, although see, Collins et al. 2016 for a different conclusion). On the other hand, modulation of the BOLD response by semantic, identity-specific information in the OFA (Amado et al. 2018), a region lower in hierarchy in the face-processing network, is more remarkable. One question that arises regarding this observation is whether the modulated activity in the OFA reflects a functional contribution of this area in associative identity processing, or is merely an epiphenomenon.

Here, we tested the functional relevance of the OFA in cross-domain identity priming using a state-dependent TMS paradigm to answer this question. In a previous study (Ambrus et al. 2017a, b) using face images as stimuli, we observed the disruption of identity-specific priming (facilitated performance for different identity target images) by TMS of the right OFA. In the current study, similarly to Amado et al. (2018), primes were names and targets were photographs of famous public figures, and the task was a familiarity decision for the faces. Our present results show a similar effect—the intact priming effect in the vertex control condition (a difference in accuracy between congruent and incongruent trials) is reduced by TMS of the rOFA, due to the increased accuracy in the incongruent condition.

State-dependent TMS

Recent theories suggest that the effect of TMS depends on the prior state of neurons: it facilitates the less active or less excitable neuron populations stronger than the more active ones (Cattaneo and Silvanto 2008a, b; Silvanto 2008). Indeed, in our previous face priming study we observed an increase in accuracy in the non- primed condition (when a face was preceded by another, unrelated face) in the rOFA as compared to the vertex TMS condition (Ambrus et al. 2017a, b). We reasoned that TMS elevates the activation level of those neurons that are not activated by the prime and thereby it aids the processing of non-primed stimuli, leading to better performance. We argue that the results of the current study further support this hypothesis by showing that only the incongruent trials were affected by the TMS of OFA, which showed an increased performance when compared to the vertex control condition. In comparison with a congruent name-face stimulus pair, where the name activates the same identity representation as the subsequent image the incongruent primes lead to less prior activation. This lower activation, in turn, makes incongruent trials more susceptible to state-dependent TMS effects, and this leads to enhanced performance. This further emphasizes the importance of state-dependent TMS in understanding cortical representations on a finer spatial scale where conventional stimulation techniques are not efficient anymore.

Cross-domain name-face priming

While stimulus repetition related priming is frequently used in cognitive neurosciences to study various perceptual and mnemonic processes of face perception [for reviews of neuroimaging and electrophysiological studies see (Henson 2003; Schweinberger and Neumann 2016)], it is surprising that hardly any electrophysiological studies applied cross-domain name-face priming paradigms in the past (for a recent neuroimaging study see Amado et al. 2018). Jemel et al. (2005) measured ERPs in a within and cross-domain self-priming paradigm and found that the N170, an early face-sensitive component of face perception (Bentin et al. 1996) and a later component between 400 and 800 ms were modulated equally by both, while a medium-latency ERP component between 200 and 400 ms post-stimulus onset was only present for within-domain priming. The authors concluded that priming-related processes, common to within and cross-domain priming as well as non-priming specific processes, such as the incidental recollection of semantic information, are reflected in the responses. Two additional studies used cross-domain semantic priming, where target faces were preceded by associated or non-associated names, e.g. the face of Brad Pitt was preceded by the name "Angelina Jolie" or "John Lennon"; (Wiese and Schweinberger 2008, 2011) and these semantic priming effects were also found to be associated with later components between 300 and 600 ms. Taken together, these studies highlight the role of later, semantic processing and suggest that the conflict of perceptual–semantic integration leads to cross-domain priming effects (Holcomb and Neville 1990; Nobre and McCarthy 1994; Chwilla et al. 1995; Matsumoto et al. 2005).

To the best of our knowledge, the current study is so far the only to test cross-domain priming using TMS. Therefore, it is of great theoretical importance that the stimulation of an "early" face processing area is able to alter cross-domain identity priming effects. How semantic information reaches the right OFA is an open question as of today. The finding that the OFA plays a role in the semantic information processing of identity cannot be explained by feed-forward, low-level response adaptation mechanisms, as there was no direct stimulus repetition in our paradigm. Rather, it is more probable that semantic information reaches the occipital cortical areas via cortical feedback. Indeed, Jemel et al. (2005) in their above-mentioned cross-domain priming study suggested that the early N170 effect reflects top-down influences from the representational system. While this question will require more detailed and specifically targeted experiments it has been already proposed previously that the rOFA receives strong re-entrant feedback information about faces (Pitcher et al. 2007, 2012; Kadosh et al. 2011), presumably from the visual letter-form area (LFA) (Thesen et al. 2012), visual word-form area (WFA) (Cohen et al. 2000, 2002; Dehaene et al. 2002) or anterior and medial temporal cortices. In line with this theory, recent functional connectivity studies showed that there is a considerable proportion of shared connectivity between the WFA and FFA (Bouhali et al. 2014). Additionally, it has also been shown that the FFA is activated by familiar auditory stimuli (Kriegstein et al. 2005), suggesting a multimodal, higher-level identity representations in this area and this information may fed back to OFA as well, explaining the current cross-domain identity priming modulation.

The role(s) of the OFA in the face perception network

It is fairly well established that the OFA plays a role in the early stages of face processing, constructing a low-level representation of facial features (Pitcher et al. 2007, 2008). Hierarchical models of face perception postulate that information then flows from the OFA to higher level regions (Haxby et al. 2000; Zhen et al. 2013), increasing in the level of abstraction. Accumulating evidence, however, increasingly calls into question the strictly hierarchical and specialized organization of the face perception network. It has been shown that OFA impairment may result in prosopagnosia-like symptoms (Rossion et al. 2003; Bouvier and Engel 2006) and that without contribution from the rOFA, the rFFA does not discriminate individual faces properly (Schiltz et al. 2006; Dricot et al. 2008). Intracranial electrical stimulation of the rFFA, but also of the rOFA elicits transient impairments in face matching and recognition, in addition to distortions of the face percept (Jonas et al. 2012, 2015, 2017). Furthermore, higher-level regions, such as the rFFA, have been shown to be activated in the absence of input from the rOFA following brain damage (Rossion et al. 2003; Steeves et al. 2006; Rossion 2008). More recently, it has been reported that atypical faces elicit larger responses compared to typical faces in the posterior occipito-temporal cortex, including the OFA, but not the FFA. This has led to the proposal that the FFA exerts modulatory influence on the activity of the OFA via inhibitory sculpting (Engell et al. 2018). Finally, in a recent study it has been demonstrated that disrupting processing in the right OFA during learning by TMS impairs face-identity acquisition in a sorting and matching task (Ambrus et al. 2017). These findings together strongly suggest that the OFA is necessary for the image-invariant identity processing of faces and is not merely an entry point of the face perception network. Based on this evidence, feedback interactions between the rFFA to the rOFA have been proposed for establishing a full individual face percept (Rossion 2008). The modulation of the cross-domain identity priming by OFA TMS suggests that this area plays a causal role in the association of names and faces. Therefore, similarly to Ambrus et al. (2017) and to certain novel models of face perception (Duchaine and Yovel 2015), we suggest that the OFA might be crucial to person recognition by playing a role in the association of visual facial and semantic information.

In the present study, we demonstrated that TMS stimulation of the rOFA does not only influence identity-dependent priming for face stimuli (Ambrus et al. 2017a, b), but it also affects cross-domain semantic priming of faces by names. This suggests that populations of neurons exist in the rOFA that take part in semantic processing of identity, probably in interplay with other nodes in the extended face network and beyond, involving synchronized feed-forward and feed-back modulation.

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Compliance with ethical standards

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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