

THE ROLE OF OCCIPITAL TEMPORAL CORTEX IN THE FORMATION OF FACE FAMILIARITY AND IDENTITY



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Summary

Faces hold a special role in human cognition. Recognizing familiar faces and differentiate between different identities is crucial for any social interaction. Faces are visually identified along the 'ventral stream' in the occipito-temporal pathway. Face perception has been separated into a core and extended network depending on the underlying processing in the 'model of the distributed human neural system for face perception' (Haxby et al., 2000). One region of the core-network is the Occipital Face Area (OFA), which has been previously described as a low-level, structural encoding area (Pitcher et al., 2007; Liu et al., 2010; Duchaine and Yovel, 2015). The topic of this work is to investigate whether the OFA plays a more complex role in face processing, as recent studies suggest (Ambrus et al., 2017a,b, 2019a). The focus hereby lays on the differential processing of familiar and unfamiliar faces and their identity representations.

In the course of this Thesis we will present and discuss four studies conducted to answer the following research questions:

- I. Is the OFA participating in the formation of image-specific and image-invariant face representations?
- II. Can we get familiarized with previous unknown faces via semantic information and is the bilateral OFA involved in this process?
- III. What are the temporal dynamics of familiarity and identity learning in three different categories in electrophysiological responses?
- IV. Can we detect the different processing of familiar and unfamiliar faces in neural components and are these processes modulated by the OFA?

Study I evaluated whether image-specific and image-invariant identity representations of ambient face images are traceable in the right OFA. We presented face images while transcranial magnetic stimulation pulses (TMS) were applied over the rOFA during a face encoding phase of a memory task. Participants were trained on one identity with 30 different images while 30 images of different identities were presented a single time. In a subsequent retrieval phase, recognition memory was tested using a two-alternative forced-choice recognition task. We demonstrated, that TMS over rOFA impaired the encoding of trained ID images. This indicates that the occipital temporal cortex, including the OFA, is involved in the encoding of image-specific face representations and emphasizes its involvement in face recognition.

Study II then focused on a more complex function in face processing, namely the association of

semantic biographical information with a face. The experiment used TMS to test whether the OFA is involved in the association of a face with identity-specific semantic information, such as the name or job title of a person. We applied an identity-learning task where unfamiliar faces were presented together with a name and a job title in the first encoding phase. Simultaneously, TMS pulses were applied either to the left or right OFA or a control region. In the subsequent retrieval phase, the previously seen faces were presented either with two names or with two job titles and the task of the participants was to select the semantic information previously learned. We found that the stimulation of the right or left OFA reduced subsequent retrieval performance for the face-associated job titles. This suggests a causal role of the OFA in the association of faces and related semantic information and shows that this region is not limited to unimodal visual information. Furthermore, in contrast to prior findings, we did not observe hemispherical differences of the TMS intervention, suggesting a similar role of the left and right OFAs in the formation of the visual-semantic associations. Our results suggest the necessity to reconsider the hierarchical face-perception models and support the distributed and recurrent models.

In *Study III* we connected three different categories of familiarity with electroencephalogram (EEG) correlates to evaluate the neural involvement in this process. In three EEG experiments, we elucidated how representations of face familiarity and identity emerge from different qualities of familiarization: brief perceptual exposure (Experiment 1), extensive media familiarization (Experiment 2) and real-life personal familiarization (Experiment 3). Time-resolved representational similarity analysis revealed that familiarization quality has a profound impact on representations of face familiarity: they were strongly visible after personal familiarization, weaker after media familiarization, and absent after perceptual familiarization. Across all experiments, we found no enhancement of face identity representation, suggesting that familiarity and identity representations emerge independently during face familiarization. Our results emphasize the importance of extensive, real-life familiarization for the emergence of robust face familiarity representations, constraining models of face perception and recognition memory.

Study IV connected electrophysiological signals of familiar faces with the causal involvement of the OFA. We tested whether the OFA plays a causal role in the differential processing of familiar and unfamiliar faces. We used an offline, inhibitory continuous theta-burst stimulation (cTBS) protocol over the right OFA and a control site. An EEG recording of event-related potentials (ERPs), elicited by visually presented familiar (famous) and unfamiliar faces was

performed before and after stimulation. This is the first study showing the causal role of the rOFA in the differential processing of familiar and unfamiliar faces, using combined cTBS and EEG recording methods. We observed a difference in ERPs for famous and unfamiliar faces in a time-window corresponding to the N250 component. Importantly, this difference was significantly increased by cTBS of the right OFA, suggesting its causal role in the differential processing of familiar and unfamiliar faces. The enhancement occurred focally, at electrodes close to the right hemispheric cTBS site, as well as over similar occipito-temporal sites of the contralateral hemisphere. These results show the differential representations of familiar and unfamiliar faces and support an extensive, bilateral network.

The outcome of the described studies indicates, that functions of the occipital temporal cortex, including the OFA, comprise perceptual face processing, identity representations and the association to further semantic information. It proves that the OFA is not limited to only low-level feature processing, but comprises a versatile involvement in the face network. This suggests a re-evaluation of the serial and hierarchical models of face processing and favours a non-hierarchical, global-to-local model with re-entrant connections between the OFA and other face processing areas (Solomon-Harris et al., 2013).

We propose a model with reciprocal interactions between the OFA and higher face processing regions, such as the Anterior Temporal Pole (ATL). It describes top-down modulatory signals from ATL and resulting input-dependent responses from the OFA, which can be excitatory as well as inhibitory. The model captures the differential processing of familiar and unfamiliar faces and presents an explanation in regards to the underlying anatomical causes. We further conclude that the OFA is involved in the processing of both, familiar and unfamiliar faces.

Zusammenfassung

Gesichter nehmen in der menschlichen Kognition eine besondere Rolle ein. Das Erkennen von bekannten Gesichtern und die Unterscheidung zwischen verschiedenen Identitäten ist entscheidend für jede soziale Interaktion. Gesichter werden visuell entlang des 'ventral stream' in der okzipito-temporalen Bahn identifiziert. Die Gesichtswahrnehmung wurde in Abhängigkeit von der zugrundeliegenden Verarbeitung im 'Modell des dezentralen neuronalen Systems für Gesichtswahrnehmung' (Haxby et al., 2000) in ein Kern- und ein erweitertes Netzwerk aufgeteilt. Eine Region des Kernnetzwerks ist das Occipital Face Areal (OFA), das bisher als Gebiet für rein strukturelle Kodierung in frühen Prozessen beschrieben wurde (Pitcher et al., 2007; Liu et al., 2010; Duchaine and Yovel, 2015).

In dieser Arbeit soll untersucht werden, ob das OFA eine komplexere Rolle bei der Gesichtsverarbeitung spielt, wie neuere Studien nahelegen (Ambrus et al., 2017a,b, 2019a). Der Fokus liegt dabei auf der unterschiedlichen Verarbeitung von bekannten und unbekannten Gesichtern und deren Identitätsrepräsentationen.

Im Rahmen dieser Arbeit werden vier Studien vorgestellt und diskutiert, die zur Beantwortung folgender Forschungsfragen durchgeführt wurden:

- I. Ist das OFA an der Bildung bildspezifischer und bildinvarianter Gesichtsrepräsentationen beteiligt?
- II. Kann man mithilfe von semantischen Informationen vorher unbekannte Gesichter vertraut machen und ist der bilaterale OFA an diesem Prozess beteiligt?
- III. Was zeigt die zeitliche Dynamik von Vertrautheits- und Identitätslernen in drei verschiedenen Kategorien in elektrophysiologischen Messungen?
- IV. Können wir die unterschiedliche Verarbeitung von bekannten und unbekannten Gesichtern in neuronalen Komponenten nachweisen und werden diese Prozesse durch das OFA moduliert?

Studie I untersucht, ob bildspezifische und bildinvariante Identitätsrepräsentationen von Bildern von Gesichtern im rechten OFA nachweisbar sind. Wir präsentierten Gesichtsbilder zum 'Encoding' in einer Gedächtnisaufgabe, während transkranielle magnetische Stimulation (TMS) über dem rOFA appliziert wurde. Die Teilnehmenden wurden auf eine einzige Identität mit 30 verschiedenen Bildern trainiert, während 30 Bilder verschiedener Identitäten nur ein einziges Mal präsentiert wurden. In einer anschließenden 'Retrieval'-Phase wurde das

Wiedererkennungsgedächtnis mit einer 'Zwei-Alternativen Forced-Choice-Aufgabe' getestet. Wir konnten zeigen, dass TMS über dem rOFA das Erlernen der trainierten Identitätsbilder beeinträchtigte. Dies deutet darauf hin, dass der okzipitale temporale Kortex, einschließlich des OFA, an dem Aneignen von bildspezifischen Gesichtsrepräsentationen beteiligt ist und unterstreicht seine Bedeutung für die Gesichtserkennung.

Studie II konzentrierte sich dann auf eine komplexere Funktion bei der Gesichtsverarbeitung, nämlich die Assoziation von semantischen biographischen Informationen mit einem Gesicht. Das Experiment verwendete TMS, um zu testen, ob das OFA an der Assoziation eines Gesichts mit identitätsspezifischen semantischen Informationen, wie dem Namen oder dem Beruf einer Person, beteiligt ist. Wir wandten eine Identitäts-Lernaufgabe an, bei der in der ersten Lernphase unbekannte Gesichter zusammen mit einem Namen und einer Berufsbezeichnung präsentiert wurden. Gleichzeitig wurde entweder die linke oder rechte OFA oder eine Kontrollregion stimuliert. In der anschließenden 'Retrieval'-Phase wurden die zuvor gesehenen Gesichter entweder mit zwei Namen oder mit zwei Berufsbezeichnungen präsentiert und die Aufgabe der Teilnehmenden war es, die zuvor gelernte semantische Information auszuwählen. Wir fanden heraus, dass die Stimulation der rechten oder linken OFA die anschließende Abrufleistung für die gesichtsassoziierten Berufsbezeichnungen reduzierte. Dies deutet auf eine kausale Rolle der OFA bei der Assoziation von Gesichtern und zugehörigen semantischen Informationen hin und zeigt, dass diese Region nicht auf unimodale visuelle Informationen beschränkt ist. Darüber hinaus konnten wir im Gegensatz zu früheren Befunden keine hemisphärischen Unterschiede beobachten, was auf eine ähnliche Rolle der linken und rechten OFA bei der Bildung der visuell-semantischen Assoziationen hindeutet. Unsere Ergebnisse legen die Notwendigkeit nahe, die hierarchischen Modelle der Gesichtswahrnehmung zu überdenken und multilaterale Netzwerk-Modelle zu unterstützen.

In *Studie III* haben wir drei verschiedene Kategorien von Vertrautheit mit Elektroenzephalogramm (EEG)-Korrelaten verbunden, um die neuronale Beteiligung an diesem Prozess zu bewerten. In drei EEG-Experimenten untersuchten wir, wie Repräsentationen von Gesichtsbekanntheit und -identität durch unterschiedliche Qualitäten der Bekanntmachung entstehen: kurzes visuelles Kennenlernen (Experiment 1), umfangreiche Bekanntmachung über Medien (Experiment 2) und persönliche Kennenlernen im realen Leben (Experiment 3). Eine zeitlich hochaufgelöste 'representational similarity analysis' zeigte, dass die Qualität der Bekanntmachung einen großen Einfluss auf die neuronalen Repräsentationen der Gesichter hat: Sie waren stark sichtbar nach persönlicher Bekanntschaft, schwächer nach medialem Kennenlernen und

nicht vorhanden nach visueller Bekanntheit. In allen Experimenten fanden wir keine Verstärkung der Identitätsrepräsentation von Gesichtern, was darauf hindeutet, dass Bekanntheits- und Identitätsrepräsentationen während des Kennenlernens von Gesichtern unabhängig voneinander entstehen. Unsere Ergebnisse unterstreichen die Bedeutung eines umfangreichen, realen Kennenlernens eines Gesichts für die Entstehung stabiler Repräsentationen der Gesichtsbekanntheit, was die Modelle der Gesichtswahrnehmung und des Erkennungsgedächtnisses einschränkt.

Die *Studie IV* verband elektrophysiologische Signale von bekannten Gesichtern mit der kausalen Beteiligung des OFA. Wir testeten, ob das OFA eine kausale Rolle bei der unterschiedlichen Verarbeitung von bekannten und unbekannten Gesichtern spielt. Wir verwendeten ein 'offline' Protokoll mit inhibitorischer, durchgängiger Theta-Burst-Stimulation (cTBS) über dem rechten OFA und einer Kontrollstelle. Vor und nach der Stimulation wurden mit EEG-Aufzeichnung ereignis-korrelierte Potentiale (ERPs) erhoben, die durch visuell präsentierte bekannte (berühmte) und unbekannte Gesichter ausgelöst wurden. Dies ist die erste Studie, die die kausale Rolle des rOFA bei der unterschiedlichen Verarbeitung von bekannten und unbekannten Gesichtern mit kombinierten Methoden von cTBS- und EEG-Aufzeichnung zeigt. Wir beobachteten einen Unterschied in den ERPs für bekannte und unbekannte Gesichter in einem Zeitfenster, das der N250-Komponente entspricht. Wichtig ist, dass dieser Unterschied durch cTBS des rechten OFA signifikant verstärkt wurde, was auf eine kausale Rolle bei der unterschiedlichen Verarbeitung von bekannten und unbekannten Gesichtern hindeutet. Die Verstärkung trat örtlich gebunden an Elektroden in der Nähe der rechtshemisphärischen cTBS-Stelle auf, sowie über ähnlichen okzipito-temporalen Stellen der kontralateralen Hemisphäre. Diese Ergebnisse zeigen die verschiedenen Repräsentationen von bekannten und unbekannten Gesichtern, das wieder auf ein umfangreiches, bilaterales Netzwerk hinweist.

Die Ergebnisse der beschriebenen Studien deuten darauf hin, dass die Funktion des okzipitalen temporalen Kortex, einschließlich des OFA, die visuelle Gesichtsverarbeitung, Identitätsrepräsentationen und die Assoziation mit semantischen Informationen umfasst. Es zeigt, dass das OFA nicht nur auf die niedrige Merkmalsverarbeitung beschränkt ist, sondern eine vielseitige Beteiligung am Gesichtsnetzwerk innehat. Dies legt eine Neubewertung der seriellen und hierarchischen Modelle der Gesichtsverarbeitung nahe und begünstigt ein nicht-hierarchisches, global-lokales Modell mit wieder-eintretenden Verbindungen zwischen dem OFA und anderen gesichtsverarbeitenden Arealen (Solomon-Harris et al., 2013).

Wir schlagen ein Modell vor mit reziproken Interaktionen zwischen dem OFA und höheren gesichtsverarbeitenden Regionen, wie dem Anterioren Temporalen Pol (ATL). Es beschreibt top-down modulierende Signale von dem ATL und daraus resultierende input-abhängige Antworten von dem OFA, die sowohl exzitatorisch als auch inhibitorisch sein können. Das Modell erfasst die unterschiedliche Verarbeitung von bekannten und unbekannten Gesichtern und liefert eine Erklärung hinsichtlich der zugrunde liegenden anatomischen Ursachen. Wir kommen zu dem Schluss, dass das OFA sowohl an der Verarbeitung von bekannten als auch von unbekannten Gesichtern beteiligt ist.

1 Recognition of Familiar and Unfamiliar Faces

1.1 The Face Network

Faces, like other objects, are visually identified along the occipito-temporal pathway, the 'ventral stream' (Ungerleider and Haxby, 1994). However, a specialized network is responsible for face processing (Collins and Olson, 2014; Pitcher et al., 2007) as conceptual knowledge of the related person is connected to the face (Lambon Ralph et al., 2009; Pitcher et al., 2009). Further, faces deviate from object processing, as faces play a unique role in the evolutionary progress of the humankind. It is crucial to correctly identify a person, as well as their intentions and emotions, which are perceivable in their face expressions. That facilitated the development of the automatic processing of faces, which was described for face recognition as well as the evaluation of facial expressions (Volfart et al., 2020; Sato et al., 2015), particularly for familiar faces (Burton et al., 2005). The fast and automated recognition of a face resulted in a holistic approach, as faces are not processed as a collection of separable facial features, but rather as an 'integrated perceptual whole' (Taubert et al., 2011; Maurer et al., 2002). Maurer et al. (2002) described three general stages of the face recognition process: First, detecting a face, based on the typical spatial relation of face parts, secondly the holistic processing, namely the integration of the facial features and third discriminating between faces, based on the prototypical spatial arrangement of each feature.

Over the years multiple models of face recognition were developed with different emphasis on cognitive or neural based components. One of the first and most criticized cognitive model is the 'functional model of face recognition' by Bruce and Young (1986). They describe individual units for the analysis of facial speech, expression and recognition which follow a rather hierarchical approach. Further, face recognition and the identification of a person are related but separate processes. As the single face recognition unit did not specify the underlying processes and because it was not based on neurophysiological data, this model was adapted by Haxby et al. (2000). They connected the functional units of face recognition and identification to neuronal correlates and developed a two-stage network model including multiple involved regions, depicted in Figure 1.

Faces get visually analysed in the core system, which is comprised of the Inferior Occipital Gyri (IOG), the Lateral Fusiform Gyrus (LFG) and the Superior Temporal Sulcus (STS). The extended system then evaluates higher face features, such as semantic and contextual infor-

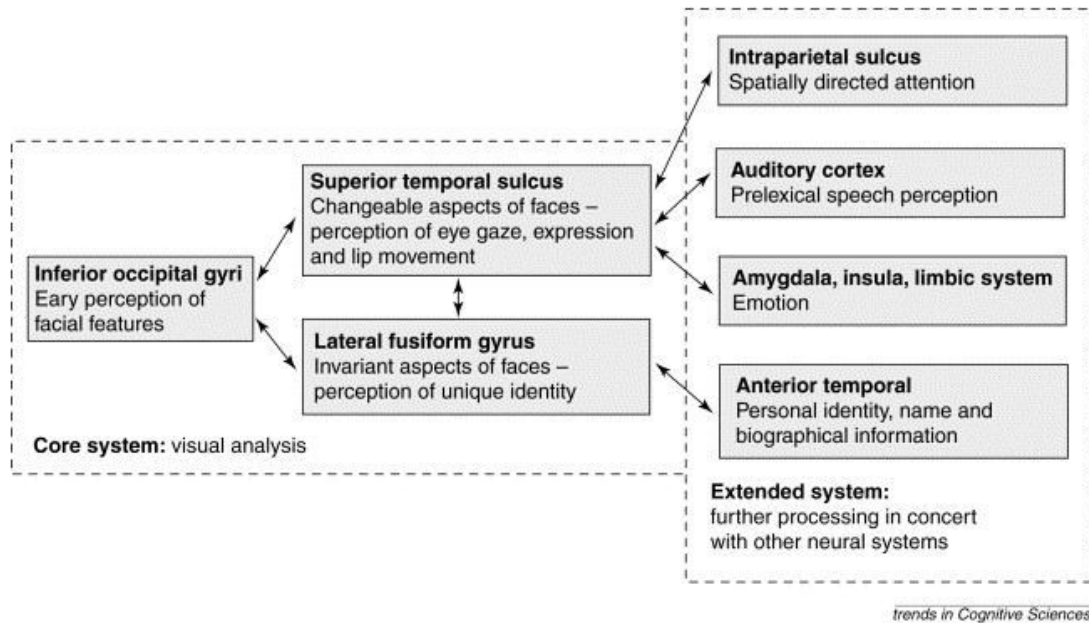


Figure 1: The first neurally motivated two-stage network model for face perception, developed by Haxby et al. (2000). The serial model is divided into a core and an extended stage, each containing several regions.

mation and emotions. The involved regions are the Intraparietal Sulcus, the Auditory Cortex, the Anterior Temporal Lobe (ATL) and Amygdala, Insula and Limbic System, all of which also play a role in other cognitive processes. As the flow of information between the core and the extended system as well as the organization within the core region, are described as serial, Haxby's model suggests a hierarchical approach in face processing as well.

Haxby's model has been further adapted by Gobbini and Haxby (2007) who distributed the extended system into regions involved in emotions and person knowledge. Additionally, top-down modulatory feedback loops were introduced, which gives the first insight into the complexity of the face network (Gobbini and Haxby, 2007). Duchaine and Yovel (2015) then connected the IOG and LFG of the core network to the previously defined face-selective areas Occipital Face Area (OFA) and Fusiform Face Area (FFA) and revised the two-stage model to a more complex and region-based framework. They incorporated the ventral and dorsal face-processing pathways into their model and introduced multiple feed-forward and -backward connections based on functional connectivity. But individual tasks are still processed in one single component of the model, for example the identity processing in the LFG. That is a simplified approach, as most functions are reached through the cooperation and interaction of various regions.

To get an overview about all involved regions of the face network, in Figure 2 all cortical and

subcortical areas are depicted and colour-coded in regards to their functions.

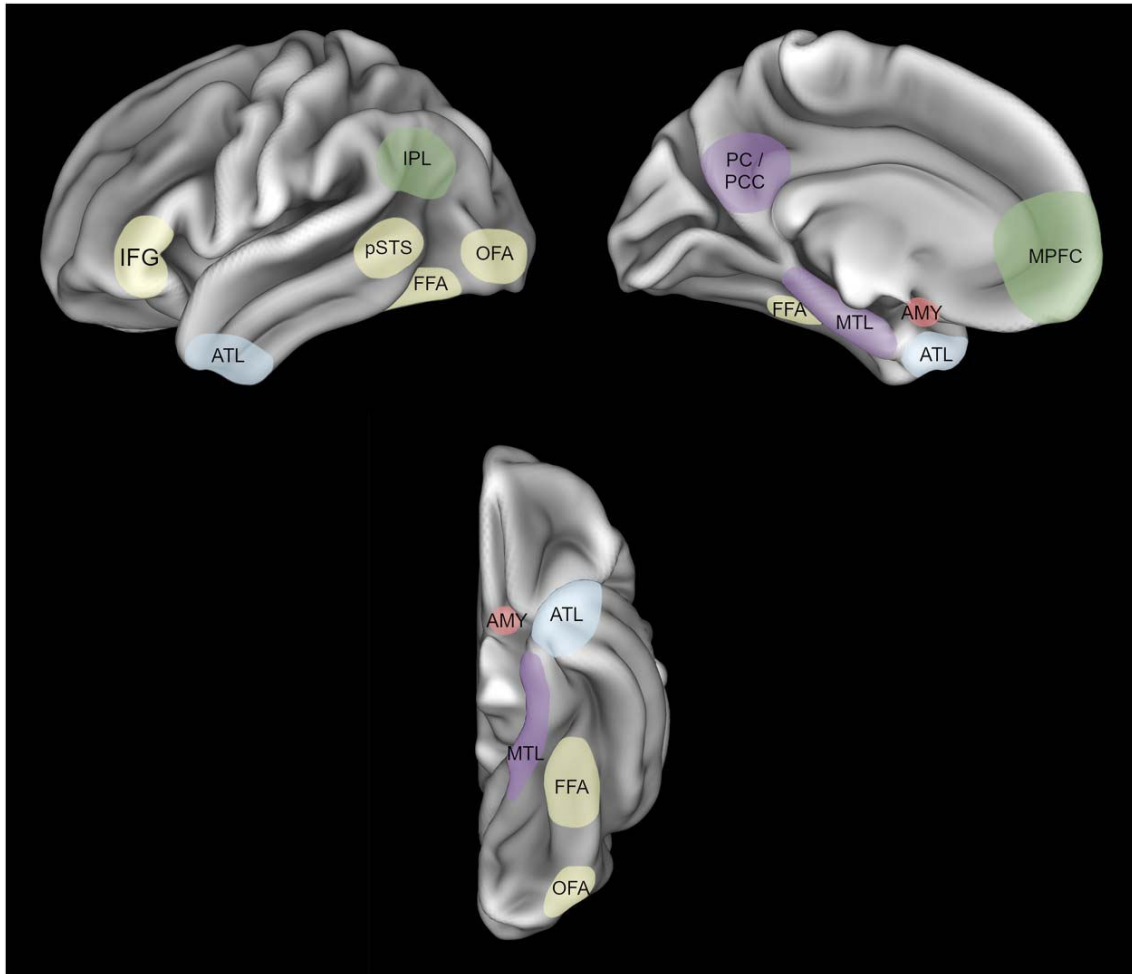


Figure 2: Cortical and subcortical areas of the face network, created by Kovács (2020). Yellow areas depict the involvement in recognition memory, areas of the core face processing network are tinted purple, blue colour shows a role in semantic processing, areas involved in social aspects, personality traits and attitudes are depicted green and a red colour codes the involvement in emotional processing (for abbreviations please see page 170). Upper left: lateral view, upper right: medial view, below: ventral view (on one hemisphere)

1.1.1 Core Network

The importance of the interaction between the regions of the face network is further described by the within-network-connectivity (Wang et al., 2016). A stronger connection of the right fusiform face area with other face-regions is correlated with improved face recognition. However also the differentiation to non-face networks is relevant since their weaker connection to the right occipital face area indicates a similar effect. Wang et al. (2016) accordingly propose a two-stage model, with the OFA being the early stage of face perception, distinguishing be-

tween face and non-face stimuli, and the FFA, as the second stage, processes the whole face information holistically together with other face-selective regions.

Occipital Face Area

This is in line with previous studies, in which the OFA is described as an early face-processing stage and the gateway of the face network (Pitcher et al., 2007; Liu et al., 2010; Duchaine and Yovel, 2015). Identity representations in the OFA are described as image-dependent (Davies-Thompson et al., 2009; Yovel and Kanwisher, 2004; Hoffman and Haxby, 2000) and the OFA is reported to preferably represent the facial components of a face (eyes, nose, mouth) (Pitcher et al., 2011). Hence, this region is seen as an early stage of visual perception and rather not involved in the processing of more complex facial features (Pitcher et al., 2011; Nichols et al., 2010). This early involvement is also shown in transcranial magnetic stimulation (TMS) and lesion studies. Patients with a damaged OFA exhibit impaired face discrimination capacities (Dricot et al., 2008; Schiltz et al., 2006) and repetitive double-pulse TMS of the right OFA (rOFA) disrupts the discrimination of face parts as well as (unfamiliar) faces per se (Pitcher et al., 2007, 2009). This evidence points towards an involvement of the OFA in creating an initial representation of a face. The timing of the stimulation further gives insights into the temporal contribution of the OFA. The accuracy of face discrimination was only decreased after stimulation onset of 60 - 100 ms post-stimulus, showing a fast reaction of the rOFA to faces (Pitcher et al., 2007). The fast response of this region hints towards a role in early face processing, however, there is no evidence that the functions of the OFA are limited to it.

Accordingly, recent studies attribute a more complex role to this region. Again, TMS is utilized to detect a possible causal role of the OFA in higher-level face processing. It was shown, that the OFA is involved in the learning of novel faces as TMS over the rOFA eliminates the training effect in a face-matching task and impairs the integration of identity and expression (Ambrus et al., 2017b; Kadosh et al., 2011). Further, priming paradigms were applied, in which familiar face images were primed with either the same image, another image of the same identity, or a different face. In a related study the prime was either the correct name of the person or an incongruent name. In both experiments, TMS was applied over rOFA during target image onset. The results reveal, that stimulating the rOFA reduced the observed face priming effect as well as the cross-domain priming effect. These findings indicate a causal role of the OFA in identity specific processing and in the association between a face and the name (Ambrus et al., 2017a, 2019a). The association between the name and the face of a person in the OFA is also visible

in functional neuroimaging, by a reduced BOLD signal (blood oxygen level dependence) in bilateral FFA and OFA after cross-domain priming of a familiar face with its name, which goes along with a facilitated recognition (Amado et al., 2018).

Hence, today it seems that the participation of the OFA is not limited to visual facial information but already retrieves identity-specific knowledge. The experiments described in this Thesis, will further elaborate on the versatile role of the OFA in the face network and give new prospects to the organisation of related models.

Fusiform Face Area

Strong structural white matter connections have been found between the OFA and the FFA, which is also part of the core in the two-stage network model (Fig. 1, p. 15) (Pyles et al., 2013; Haxby et al., 2000). The FFA was first described by Kanwisher et al. (1997) as a region ‘that responded significantly more strongly during passive viewing of face than object stimuli’. Since then, the function of the FFA in face processing has been refined, as it is related to holistic face perception in general while not being influenced by low-level information (Collins and Olson, 2014; Kanwisher and Yovel, 2006). Gauthier et al. (2000) report a habituation/adaptation effect after presenting different images of the same individuals hinting towards invariant face representations in the FFA. Further, a MVPA study associated the recognition of famous faces with neural patterns in the FFA (Axelrod and Yovel, 2015). These results altogether suggest that individual faces are already discriminated at the level of the FFA.

Superior Temporal Sulcus

The third region of Haxby’s two-stage network model is the STS, which is involved in the processing of dynamic features of face perception (Fig. 1, p. 15). This area is activated by non-static information, namely changeable aspects such as facial expression, eye gaze and lip movements (Puce et al., 1998), hence supports social interaction.

1.1.2 Extended Network

Anterior Temporal Lobe

Another unit of the face network (Fig. 2, p. 16), crucial for social interaction is the anterior temporal lobe, also named anterior face patch (aFP) (Harry et al., 2016; Rajimehr et al., 2009). It

is a part of the extended system of Haxby's model and plays a role in high-level face processing. That manifests in an affected feeling of familiarity for famous faces after the stimulation of the right ATL (Ranieri et al., 2015). This region is considered to be involved in connecting the visual representation of a face to the corresponding semantic knowledge (Chiou and Lambon Ralph, 2018; Rice et al., 2018; Tsukiura et al., 2010). The ATLs participation in encoding and retrieving semantic information of a person exhibits a left hemispherical dominance, as familiar faces evoke a stronger signal compared to unfamiliar ones in the left ATL (von der Heide et al., 2013; Tsao et al., 2008). Further, the identity representation in the ATL is view-independent and affected by prior experiences (Duchaine and Yovel, 2015). Hence, social interaction is only possible by retrieving personal knowledge associated with a familiar face, such as their name or job (Fig. 1, p. 15).

Other high-level regions

Closely connected to social interactions is the person-specific long-term episodic memory and the emotional response to a person. The processes regarding affective visual stimuli and emotional responses are linked to the Amygdala and Insula, which are both part of Haxby's extended system (Ramon and Gobbini, 2018). Interestingly, Gobbini et al. (2004) described in an fMRI study that the neural response in the Amygdala was stronger to unfamiliar faces compared to famous faces and the weakest for personally familiar faces. One explanation was given, that an emotional response to unfamiliar faces led to an evolutionary advantage. The neural activity for personally known faces compared to famous faces, however, was increased in the anterior paracingulate and precuneus/posterior cingulate cortex as well as the posterior superior temporal sulcus (Fig. 2, p. 16). These areas, together with the medial temporal lobe, are associated with long-term episodic memory such as person-specific personality traits and attitudes. Thus, they are related to the 'theory of mind', the capacity to represent the mental state of others (Gallagher and Frith, 2003; Gobbini and Haxby, 2007).

1.1.3 Non-hierarchical Models

All the previously introduced models describing face processing are hierarchical systems (Bruce and Young, 1986; Haxby et al., 2000; Gobbini and Haxby, 2007). The information flow is organized serially from the early visual cortex to the OFA (detection), on to FFA (recognition) and STS, ATL and Amygdala (expression, semantics, emotions) (Haxby et al., 2000; Ishai, 2008;

Pitcher et al., 2011; Zhen et al., 2013). This strictly feed-forward approach is increasingly questioned (Atkinson and Adolphs, 2011; Barragan-Jason et al., 2013; Freiwald and Tsao, 2010). Aside from foundational features which are inherent to a clear serial processing, such as the continuously growing receptive field size (Grill-Spector et al., 2017), more complex connectivity among areas of the face network has been described recently. For instance, feedback connections between the OFA and the FFA have been reported by multiple studies (Gschwind et al., 2012; Jiang et al., 2011; Rossion et al., 2003). Further, robust structural connectivity between the ATL and the FFA as well as OFA is reported, which could indicate functional top-down connections (Pyles et al., 2013). Even high-level regions like the Amygdala is connected bidirectionally with the FFA, with enhanced communication during an identity discrimination task (Herrington et al., 2011). Hence, distributed and recurrent models for object and face perception need to be discussed and refined, for example, the ‘reverse hierarchical neural model of individual face perception’ (Rossion, 2014; Kravitz et al., 2013).

1.2 Development of Face Familiarity

Perhaps the most important task of a face perception network is to recognize and identify familiar persons, we know already. Getting to know a person and the associated face is an automated process in our daily routine. Besides the most common way to ‘learn’ a face via personal interaction, we can also get acquainted with a face through variable exposure over the years, which is supported by learning additional contextual and semantic information. To know a person and a solid neural representation of the related face is possible without seeing him or her once in real life. Celebrities and other people in the public eye are an inherent part of our society, which leads to a database of familiar faces for a whole culture group. This level of familiarity, however, is not comparable to personally familiar faces as the relationship is unidirectional and without the possibility of a mutual interaction (Kovács, 2020).

Familiarizing a face artificially is a method, often used in experimental settings of face or memory research. This type of familiarization can be reached through multiple image repetitions (Natu and O’Toole, 2015) or video presentation (Hahn and O’Toole, 2017). Furthermore, additional contextual information is often connected to the face to reach enhanced familiarization (see 2.1 for a detailed description) (Tsukiura et al., 2010).

Accordingly, face familiarity has been divided into three categories: personally familiar faces, the familiarity for famous faces, and reaching face familiarity via visual exposure. These cat-

egories indicate that one can become familiar with faces in different ways (Natu and O'Toole, 2011). Additional to the three introduced types of familiarity, a recent review defined another type, namely becoming semantically familiarized via personal, semantic or episodic information about the person (Kovács, 2020). It is further proposed that all these differently familiarized faces 'activate the same network but to a different extent' in regards to the distributed neural model of familiar face recognition (Gobbini and Haxby, 2007). Further, it is crucial that even though there are qualitative differences between the familiarity categories, the levels are not strictly serially organized. None of the category is simply a prerequisite to the more advanced, but describes a unique level of familiarity.

Hence, the comparison between the different levels of face familiarity or any scientific conclusions from one type to the other is a delicate matter as the face per se is processed in the same network but its learning is based on different features.

These various levels of face familiarity manifest in distinct behavioural responses as well as in different neural correlates. This hints towards a differential processing of faces in various familiarity levels, which is clearly visible when comparing responses to familiar and completely unfamiliar faces.

When confronted with several images of multiple persons with various viewpoints, face expressions and lighting in a card-sorting task, grouping the face images of the same individual together seems to be very difficult, which is not the case for familiar faces (Andrews et al., 2015; Jenkins and Burton, 2011). The recognition of a face under varying (different lighting, viewpoints, face expression) or even suboptimal circumstances (bad lighting) is only possible for familiarized faces but not for unfamiliar ones. That is due to the neural representation of a face, which develops over the years by seeing it under different lighting, viewpoints and ages, leading to a 'hallmark' of this face (Wiese et al., 2019; Burton et al., 2011). Corresponding, Gobbini et al. (2013) report a faster detection of personally familiar faces compared to unfamiliar ones.

Additionally to the visual sensory input, the associated non-visual knowledge is immediate and automatically activated when seeing a personally familiar face (Gobbini and Haxby, 2007; Kovács, 2020). This attached information, such as the semantic knowledge about and personality traits of a person, are reported to be connected with the visual representation of the face in the ATL (Chiou and Lambon Ralph, 2018; Rice et al., 2018; Tsukiura et al., 2010). Hence, besides the core face network, personally familiar faces further activate regions that are associated with

semantic, episodic or emotional processes (Natu and O'Toole, 2011). These regions involved in emotions and social attitude are the Insula, Amygdala, Hippocampus as well as anterior and posterior cingulate, medial orbitofrontal, inferior frontal and perirhinal cortex (Góngora et al., 2019; Platek et al., 2006; Leibenluft et al., 2004; Ramon et al., 2015; Taylor et al., 2009; Vila et al., 2019).

Previous studies evaluating the familiarity of a face state that this feature is encoded early in the core network and being modality-specific (Blank et al., 2014; Bruce and Young, 1986). The studies summarized above however show, that familiarity, dependent on the type, is also memory- and personality-related, hence also involving higher face processing steps.

The cortical differences of different familiarity levels are reflected in a more distinct N250 component (see 1.4.1 *Event-related Potentials*) to personally familiar faces compared to responses evoked by celebrities and lesser-known personally familiar faces like university professors (Wiese et al., 2019). The visibility of familiarity in neural responses is further supported by a review reporting larger BOLD responses in the core and extended system for famous compared to unfamiliar faces (Natu and O'Toole, 2011). As of yet, it is not possible to reach a similar level of familiarity like personally known faces in experimental settings. Accordingly, artificially familiarized faces through multiple image repetitions only activate the core network (OFA, FFA) and parietal areas (precuneus) in comparison to unfamiliar face activation (Natu and O'Toole, 2015).

In the paragraph above, the different processing of the various levels of familiarity is described. Despite the seamless transition between the stages, their neural correlates seem to be differentiable. However, it is crucial to keep in mind, that familiarity is 'not the result of all-or-none effect' (Clutterbuck and Johnston, 2002) but rather a continuum between the two categories 'known' and 'unknown'. Hence every comparison between the same or different levels of familiarity has to be made very carefully with the different background in mind.

Besides the neuronal correlates of familiarity levels, less is known about the cortical process of becoming familiar with a face. How does the representation of a face unfold in the procedure of 'getting to know' someone? A cortical transition depending on the familiarity of a face is the amount of processing depending on the image-level information (Johnston and Edmonds, 2009). Novel faces are rather processed based on the pictorial approach (Burton et al., 2011), hence image-dependent, familiar ones however are accompanied with a view-independent, neural representation of the face and are accordingly image-invariant. This shift is located

within the core network and associated with the contextual information one holds about a face and which is relevant for person identification (Schwartz and Yovel, 2016, 2019).

1.3 Face Identity

The identification of the face of a person, compared to the feeling of familiarity with it, is based on a more complex process. Familiarity is the knowledge, that you have seen a face before, even if the information of when and where is not recollectable. The identity of a face, however, is dependent on explicit knowledge about the person, such as the name, the occupation or when and where you met. These two processes are closely related and can not be separated when getting to know someone. However, they depict different stages in this process, with familiarity ongoing earlier and identity being the result of a higher processing step of recognizing a face. This is observable in electrophysiological studies, which report event-related potential (ERP) effects for familiarity but not for identity (Andrews et al., 2017; Wiese et al., 2019; Wuttke and Schweinberger, 2019). To reveal the more subtle changes in identity recognition a more sensitive analysis like multivariate pattern analysis (MVPA) has to be utilized (Ambrus et al., 2019b). This shows, that when comparing familiarity effects of faces, the identity representations of the involved faces might be recollected to some degree as well (Kovács, 2020).

Investigating face recognition with the focus on memory performance, Yonelinas (2001, 2002) defined two separate processes, familiarity and recollection. Familiarity is rather the feeling of having seen a face/stimulus, whereas recollection is accompanied with a specific memory of associated non-sensory, episodic information. It is assumed, that familiarity is a signal detection process, recollection on the other hand, is a threshold retrieval process (Yonelinas et al., 2010; Yonelinas, 1994).

1.4 The Temporal Dynamics of Face Recognition

To recognize a face quickly has been crucial in the history of humankind to differentiate friend from foe. Recognizing a face 200 ms earlier may be essential for surviving, as a fast reaction to dangerous people is necessary. Accordingly, the temporal dynamics of face processing is an interesting and important part of this research strand. Hence, to investigate this question non-invasive methods with a good temporal resolution, such as Electroencephalography (EEG) or Magnetoencephalography (MEG) are utilized (for a detailed description see 2). In the follow-

ing paragraph, uni- and multivariate analyses of these methods in face research are discussed and evaluated regarding the temporal dynamics of face processing.

1.4.1 Event-related Potentials

The first event-related potential (ERP) response to objects like faces, cars or scrambled versions of them can be measured already 100 ms post stimuli onset in a positive deflection over posterior sides, called P1 (Schendan et al., 1998; Wiese et al., 2008). It is commonly described to be sensitive to low-level features like contrast and brightness and shows dominance in the right hemisphere (Rossion and Caharel, 2011). After presenting face images, an initial steep negative deflection is seen 170 ms post stimuli onset, the N170 component. This component is interpreted as a response to face detection, as stronger ERPs, as well as adaptation effects, have been shown for faces in comparison to houses, butterflies or even similar-looking objects, like eggs (Amihai et al., 2011). This early component has not been reported to be influenced by familiarity (Eimer, 2000; Gosling and Eimer, 2011; Bentin and Deouell, 2000; Wiese and Schweinberger, 2008), but see Alonso-Prieto et al. (2015) for another conclusion. The N170 falls in the same time in which the OFA receives re-entrant feedback information at a mid-latency processing stage, around 170 ms (Kadosh et al., 2011). Spatially, electrophysiological responses to faces are generally reported over bilateral occipital-temporal poles (Jacques et al., 2019; Gosling and Eimer, 2011; Bentin and Deouell, 2000). In the same time-frame as the N170, but over a different cortical area, the vertex positive potential is mentioned, a positive deflection in the Cz electrode (Jeffreys, 1989). Stronger ERP response to faces compared to other objects hint towards an inverse correlation with the N170, like two effects of the same process (Joyce and Rossion, 2005). A later face-related ERP component appears 250 ms post stimuli onset and the following 200 - 400 ms. A hollow negative deflection, the N250, is not only specific for faces compared to other objects, but also shows different amplitudes for familiar and unfamiliar faces (Gosling and Eimer, 2011; Wuttke and Schweinberger, 2019; Wiese et al., 2019). That points towards higher face processing, in which face familiarity is already evaluated in the first 250 ms after seeing a face. Kaufmann et al. (2013) and Neumann and Schweinberger (2008) report that the visible effect is already a sign of facial identity processing. This component is located over occipital-temporal regions as well, however with tendencies towards anterior areas of the temporal pole (Wiese et al., 2019), which reflects higher face processes.

The late occipitotemporal negativity (LN) from 400 to 800 ms, follows close upon the N250

(Wuttke and Schweinberger, 2019), which makes the transition between the two components seamless. It shows effects for the 'typicality' of a face (distance to norm ratio) and face familiarity, which is why it is also labelled the sustained-familiarity effect (Wiese et al., 2019). It is closely related with the N400, showing a maximum over parietal-central electrodes, which is associated with semantic memory processing and their integration with related familiar faces (Eimer, 2000; Kutas and Federmeier, 2000; Neumann and Schweinberger, 2008).

The introduced studies describe a modulating effect of face familiarity on correlates measured over the occipital-temporal cortex. The measurable influence of face identification, however, is a more debated subject. Hence, to detect the subtle processes connected to face identity, in the next paragraph we will discuss the multivariate pattern approach in face research.

1.4.2 Multivariate Pattern Analysis

A more sensitive approach, compared to univariate ERPs, is the decoding of neural responses using machine learning algorithms. Accordingly, recent studies implemented this technique to analyse EEG, MEG or fMRI data to recognize subtle face-related processes. The multivariate approach offers the evaluation of multiple variables, like the identity and the gender of a face, within the same neural response (for a detailed description of this method see 2.3).

Neural representation of familiarity have been reported in decoded single-trial ERPs from 140 to 160 ms and from 250 to 700 ms with increasing accuracy (Barragan-Jason et al., 2015). The analysis of dense MEG recordings in occipital temporal electrodes lead to an earlier distinction of neural responses to familiar and unfamiliar faces from 100 to 350 ms (Ehrenberg et al., 2020). However, also later decoding related to familiarity have been shown in a similar study from 400 to 600 ms. This results demonstrates that traces of familiarity can be decoded after image-invariant identity information is extracted (Dobs et al., 2018).

Aside from face familiarity representations detectable with MVPA, the identification of a face, based on explicit knowledge about the person, is also traceable with this method.

The differential cortical processing of various identities is decodable within the first 200 ms after stimulus onset, for both familiar (Dobs et al., 2018) as well as unfamiliar faces (Vida et al., 2017; Nemrodov et al., 2016, 2018). Also, identity representations based on media exposition are decodable after around 90 - 250 ms post-stimulus onset (Dziura and Thompson, 2020).

These early correlates of facial identity seem to be rather explained by low-level visual features between the identities and not by explicit knowledge about this person. Hence, they are based on image-specific identity representations and are modulated by gender differences (Ambrus et al., 2019b). This is supported by Dobs et al. (2018), who report that the facial information regarding gender and age is perceived before identity in coarse-to-fine processing of face dimensions. These facial features however are recognized earlier in familiar compared to unfamiliar faces, as the familiarity of the face could enhance the bottom-up process in the face representations.

Later identity representations around 400 ms after stimulus onset are then related to the invariant coding of face identity (Ambrus et al., 2019b). These correlates may be linked to the retrieval of declarative memory information for specific individuals and activations in anterior temporal regions (Quiroga, 2012; Rey et al., 2020). Ambrus et al. (2019b) report a gradual emergence of face identity with an increasing degree of invariance, predominantly in the right hemisphere. They specify that this consistency evolves in two properties of identity representations: the equal discrimination of identities (within and between the own gender) and the tolerance to image-based variations. Hence, these later identity correlates can be attributed to image-independent representations.

The studies introduced above, investigating the temporal dynamics of cortical face processing, reveal a complex and highly specific evaluation process. They suggest that both earlier feed-forward, as well as later feedback processes, are relevant in the identification of a face (Dobs et al., 2018; Di Visconti Oleggio Castello et al., 2017; Wiese et al., 2019). Further, familiarity and even identity are recognized after 400 ms, which is a striking performance. However, when this information is embedded in the everyday situation of looking across a crowd and easily spotting a familiar face along with all other faces, this ability appears normal.

2 Methods

The methods used in cognitive neuroscience to study face processing are as versatile as the research questions themselves. Hence, for every study an individual approach has to be developed. In our case, that includes paradigms to reach and test various levels of familiarity, evaluating causal involvement by implementing virtual lesions and recording electrophysiological responses to faces. Accordingly, in the following paragraph it is detailed described how to reach face familiarity and identity within an experimental setup, how to detect a causal relationship between a cognitive task and a cortical region using TMS and why measuring EEG during face processing is a beneficial approach.

2.1 Reaching Face Familiarity and Identity

Face familiarity can be separated into four categories, based on the modality of the process: personally familiar faces, the familiarity for famous faces, becoming semantically familiarized via personal or episodic information and reaching face familiarity via visual exposure (Natu and O'Toole, 2011; Kovács, 2020). All of these familiarity groups have been examined in cognitive research.

Using personal familiar faces as stimuli in an experiment can offer rewarding results, as personal familiarity is reliable and leads to robust representations (Wiese et al., 2019). However, a close control of the familiarity level is necessary and the emotional response to the face could bias the results. It is also accompanied by great effort, because the stimulation images have to be collected, prepared and included in the experimental program for each participant individually. Hence, it is more common to use familiar faces as stimuli who are known to all participants, such as celebrities or politicians. With this approach, only cultural differences have to be considered, which can also offer additional advantages. Celebrities from another country, who are unknown in the participant group can be used as an unfamiliar counterpart in the stimuli set. Furthermore, the experiment containing the same stimuli set can be implemented in a cross-cultural setup. Accordingly, the stimulation of the same face is perceived as familiar in one cultural group and as unfamiliar in the other, which can test the response to familiarity in two unrelated cultural groups in the sense of double dissociation. When working with already familiar faces, such as celebrities or friends and family, their level of familiarity needs to be evaluated and controlled in the participant group (Biederman et al., 2018). That is realised with questionnaires retrieving the familiarity status ('Please indicate how well you

know this person on a scale from 1 to 5') or inquiring known information about the presented persons ('Please write the name, profession and any further information you know of this person').

Reaching face familiarity with repeated visual exposure and learning further contextual or episodic information about the person is a process visible in a pen pal friendship. The same approach is often used in experimental settings to familiarize faces artificially. Participants get repeatedly exposed to images of a face while performing either a face-related memory task (intentional encoding) or an unrelated attention task (incidental encoding) (Kovács, 2020). In most studies, familiarization is achieved by presenting multiple various still images of the individuals (Andrews et al., 2015; Natu and O'Toole, 2015; Ritchie and Burton, 2017), however also video clips of the person can be utilized (Hahn and O'Toole, 2017; Megreya and Burton, 2008). Of more importance than the visual medium, however, is the amount as well as the variability of the shown images. Andrews et al. (2015) showed, that a larger number of images presented per identity improves subsequent recognition in a card sorting task. It further enhances performance, when the number of present identities is known to the participants. This facilitation of face recognition is presumably due to the enhanced within-person image variability across luminance, orientation, and other low-level features. This effect can also be seen in a study by Burton et al. (2005), in which the average of multiple images of the same face leads to a more stable face representation. The effect of transient traits is lessened by the statistical mean, which in turn conserves the consistent aspects of the face (Jenkins and Burton, 2008). This form of familiarisation is purely based on low-level, pictorial features of the faces and is a good approach to test an early step of the familiarisation process.

When the images get accompanied by episodic or semantic person-specific knowledge during the learning period, faces can get familiarized semantically. This mostly fictional biographical and contextual information is administered either acoustically or visually along with the faces. That was done by Goesaert and op de Beeck (2013) in an fMRI-MVPA study, in which faces were associated with personal information (name, occupation and activity) as well as scenes to imitate spatial contexts. Familiarized and unfamiliar faces were associated with different neural patterns in OFA, FFA, and ATL (Goesaert and op de Beeck, 2013). Also Tsukiura et al. (2010) used this approach, by connecting previously unknown faces to additional, semantic information such as an individual name and job title. They could show enhanced activity

in the ventral ATL after the correct retrieval of both face-related information. Adding a 'background story' to a presented face also alters electrophysiological signals between 700 and 900 ms in left inferior-temporal electrodes (Kaufmann et al., 2009). Not only semantic knowledge but also emotional behaviour (aggressive, nice, etc.) can be experimentally associated with a face and evoke stronger activation in regions implicated in social cognition compared to novel faces (Todorov et al., 2007). This shows that, by utilizing an artificial approach, face familiarization can be reached and is traceable in face processing regions of the core as well as the extended network.

Recent studies utilize available technologies by familiarizing participants with faces/persons in the course of watching movies or series (Dziura and Thompson, 2020). Seeing the individual speak and interact offers a three-dimensional impression, while they additionally learn about his/her character in a natural setting.

Contextual knowledge as well as face image presentations are multifaceted, which leads to versatile results in the multistage process of getting to know a face (Kovács, 2020). Hence, the comparison between studies utilizing the context or image repetitions for familiarization needs to be interpreted delicately.

The studies discussed in this Thesis, involve all four types/categories of face familiarity and their experimental examination. First, we evaluated visual perceptual familiarity and identity representations in Study I. In the second Study, semantically induced familiarity and identity perceptions were examined. In Study III we then compared perceptual, media-based and personal familiarity in similar approaches. Finally, correlates of familiar (famous) and unfamiliar faces were evaluated in Study IV.

2.2 Causal Involvement of the Occipital Face Area in Face Recognition

Transcranial Magnetic Stimulation is a technique used for neuromodulation mostly in the field of basic research or treatment and investigation of diseases like major depressive disorder (Perera et al., 2016). Other than Transcranial Direct Current Stimulation (tDCS), in which a direct current is applied via electrodes, TMS utilizes electromagnetic induction with a figure-of-eight-coil to create a magnetic field with a coherent electric field. This electric field then influences the electric potential of cortical neurons by trigger an action potential. As the induced magnetic field is the size of approximately 4 cm^3 , the use is only possible in outer cortical regions

(Kammer et al., 2007). In this Thesis, we discuss the processing of visual input in occipital, occipito-temporal as well as temporal areas. To connect the stimulation with a function in a brain region a related task is necessary, for example seeing an image. The stimulation is applied in the exact time of processing, at the stimulus onset of the image. At that moment the brain region is already active due to stimulation and the processing of the image falls into the refractory period of the cells. That way, the brain region is 'occupied' and only if this area is involved in the function the normal processing is altered. Hence, a causal relationship of that area in the specific function can be assumed. The changes in the region are mostly measured in behavioural responses (accuracy, reaction time) or in combination with other methods, like EEG or fMRI.

In neuroscientific research, TMS has become a helpful tool since 1985 by modulating cortical activity (Ueno et al., 1988). It is a suitable way to induce 'virtual' lesion in healthy participants, which allows the examination of the causal role of brain areas, such as the frontal cortex, motor areas or visual regions, in various processing steps without relying on actual lesion patients (Pitcher et al., 2009; Silvanto and Cattaneo, 2017; Silvanto et al., 2010; Silvanto and Muggleton, 2008).

Nevertheless, the effect of TMS on behavioural performance is not only inhibiting but can be facilitating as well. Silvanto and Cattaneo (2017) introduced a model of state-dependent TMS effects which considered three factors that influence the nature of the outcome. First, the state of excitability in the stimulated neuron population, second the intensity of the stimulation and third the timing of the TMS application in relation to the stimuli onset.

The stimulation intensity is regarded as high or low in comparison to the phosphene threshold. That is an individual level of stimulation intensity at which stimulation over the early visual cortex elicits phosphenes (Gerwig et al., 2003). Depending on the excitability of the stimulated neuron population, low (subthreshold) or high (suprathreshold) stimulation elicits different effects, depicted in Figure 3.

The studies presented in this Thesis, all describe stimulation over neuron populations in a high excitability state, as they are potentially involved in a current task. Hence, suprathreshold stimulation was the intensity of choice. Silvanto and Cattaneo (2017) reported a mean phosphene threshold at 57.5 % of maximum stimulator output. Accordingly, suprathreshold stimulation would be at 120 % of the mean threshold which equals 69 % of maximum output.

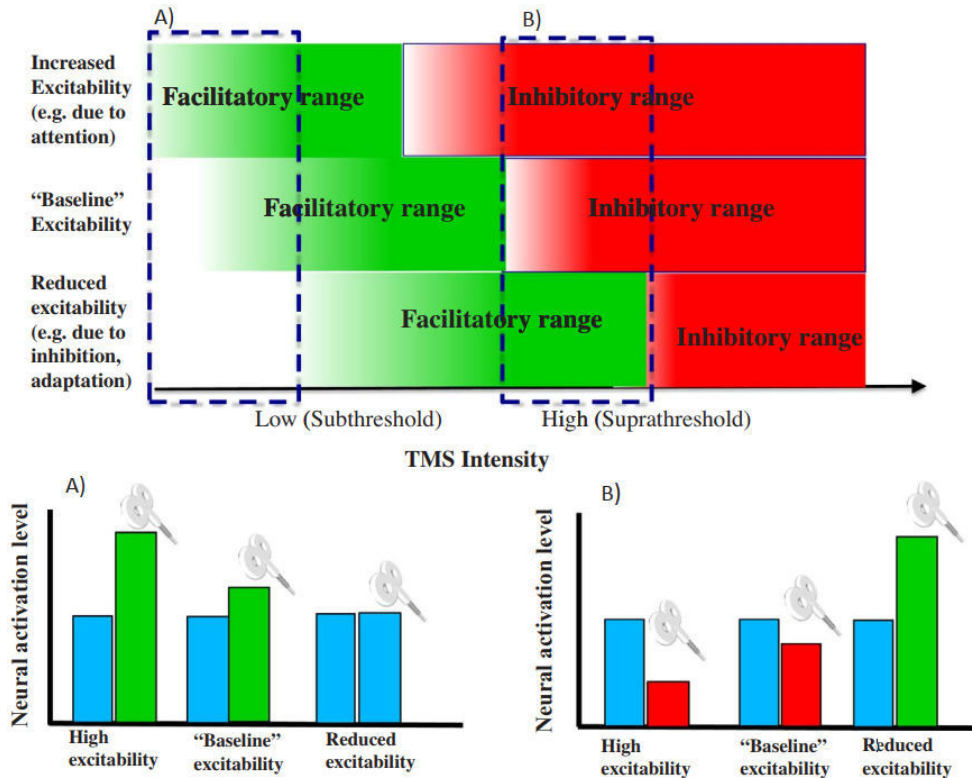


Figure 3: Facilitatory and inhibitory effects of low (A) and high (B) stimulation intensity in three neural excitability states, developed by Silvanto and Cattaneo (2017).

The stimulation intensity of 60 - 70 % is accordingly used commonly in face research to inhibit an involved brain region (Ambrus et al., 2017a,b, 2019a; Pitcher et al., 2009). This technique is called ‘online stimulation’, as it is applied selectively during the experiment, hence at the same time as the processing of a face takes place.

Another approach, used in Study IV, is to apply TMS not at stimulus onset but continuously prior to the experiment, which is called ‘offline stimulation’. For this purpose, mostly continuous theta-burst stimulation (cTBS, 300 trains á 3 pulses with 200 ms inter-train interval) is delivered continuously for a longer amount of time (20 - 60 s) (Chiou and Lambon Ralph, 2018; Bonni et al., 2015; Huang et al., 2005). In this case, subthreshold stimulation at 80 % of the mean threshold is reasonable, which translated to 40 - 45 % maximum stimulator output (Chiou and Lambon Ralph, 2018). Instead of interfering with the stimulated brain region during the time of processing as in online stimulation, offline stimulation rather fatigues the region for a longer amount of time. The excessive activation due to TMS empties the supply of sodium and potassium in the neurons which are necessary for firing. During the time they need to be restocked for the proper cell function, this neuron population is altered. That is reported to be up

to 20 minutes post-stimulation time, in which then experiments take place (Huang et al., 2005; Brückner et al., 2013; Tarnutzer et al., 2013). This approach offers the opportunity to combine TMS with other electrophysiological or imaging methods, like EEG, MEG or (f)MRI. Online stimulation would interfere with the recorded EEG signals and the coil could be a potential danger in the magnetic surrounding of the scanner. Therefore, offline stimulation prior to the measurement is one way to evaluate whether TMS induces inhibitory or excitatory effects on the measured neural responses.

In three of the four studies described in this Thesis (Study I, II and IV), transcranial magnetic stimulation was applied to reach an inhibition effect over the underlying stimulated areas. The focus of all these studies was the evaluation of a causal involvement of the occipital face area in the formation and processing of three types of face familiarity (perceptual, contextual and famous). The experiments described in Study I and Study II included online stimulation during distinct face-learning paradigms. The altered behavioural performance then allowed for conclusions. In Study IV offline TMS was combined with face-related EEG measurements before and after the stimulation of the OFA (and a control region). Hence, the comparison of electrophysiological responses of face processing with a functioning and an altered OFA is possible.

2.3 Electrophysiological Correlates of Face Recognition

Electroencephalogram (EEG) is a method used to measure electrical changes on the scalp's surface, which allows conclusions about cortical activity (Luck, 2014). Depending on their location, the activation of neuronal nodes leads to a negative or positive charge, measurable in delicate voltage changes by electrodes. The use of EEG in cognitive neuroscience is prevalent as the temporal resolution is very accurate, in the range of milliseconds (ms) (Luck, 2014). This method accordingly is able to capture fast, dynamic, and temporally sequenced cognitive events (Hu and Zhang, 2019). As it is measuring cortical responses on the head's surface (conveying through cerebrospinal fluid, meninges, skull, skin and hair), the source localization of the signals is rather coarse. Spatial resolution hence is only in the range from 5 to 9 cm (Nunez et al., 1994).

2.3.1 Event-related Potentials

To evaluate activation patterns regarding cognitive tasks, event-related potentials (ERPs) are utilized. These are averaged voltage fluctuations or changes in specific cortical regions, related to a cognitive or neurophysiological process, for example, the recognition of a face. In this Thesis, we will concentrate on exogenous sensory components, which are elicited by a given stimulus (Luck, 2014).

Hence, the most common paradigms used in ERP studies is the visual presentation of a research-related image. Images of faces are shown for 600 to 2000 ms, either coloured or greyscale, including multiple images per condition (Wiese et al., 2019; Wuttke and Schweinberger, 2019; Gosling and Eimer, 2011). Face-related ERPs, such as the N170 and the N250, emerge reliably in various paradigms. The components are not influenced by the given experimental task, if it is face-related or an attention task (Bentin and Deouell, 2000). That hints (again) towards the automatic processing of faces and their features.

The variability of the presented images, however, are of more importance. As described above in paragraph 2.1 *Reaching Face Familiarity and Identity*, the presentation of face images with an extended variability across luminance, orientation, and other low-level features facilitate the recognition of this face. That can lead to a quick comprehension of a previously unknown face and resulting traces of familiarity or identity. Consequently, the decision regarding the view-point and cropping of the face images or the alignment of the eye-level or distance should be carefully based on the purpose of the study.

Face-related ERPs, namely the N250 component over the occipital-temporal cortex, is the focus of Study IV, described in this Thesis. This technique was chosen, as ERP components provide solid electrophysiological comparability between several conditions. At the same time it is sensitive enough to pick up changes after the presentation of additional semantic information to a face (Kaufmann et al., 2009). Further, it is a prevalent method in face familiarity research. This offers a broad basis of principles to interpret our results and multiple similar studies to compare and substantiate our conclusions.

2.3.2 Multivariate Pattern Analysis

One technique to evaluate neural representations during face recognition is the Multivariate Pattern Analysis (MVPA). Compared to event-related potentials this technique is able to detect delicate effects like subtle identity-related processes. This sensitive approach evaluates multi-

ple variables within the same neural response. When MEG or fMRI data is analysed, it enables the detection of distributed selectivity maps of specific stimuli like facial identity or familiarity (Haxby et al., 2000, 2014). When used on EEG or MEG data, however, MVPA is beneficial regarding the temporal resolution (Ambrus et al., 2019b; Dobs et al., 2018; Nemrodov et al., 2018). In regards to the experimental paradigms used to obtain the data, the approach is comparable to the ones used in ERP studies, described above. However, the subsequent analysis is what sets it apart from the more traditional ERP approach.

To comprehend the idea of this analysis process, it is briefly outlined subsequently (for a detailed description see Ambrus et al. (2019b)).

First linear discriminant-analysis classifiers get trained by utilizing machine learning. These algorithms apply linear classification analysis (LCA) on collected neural response data in a leave-one-trial-out scheme. They get trained on a fraction of the data and then sort the residual data into appropriate multivariate patterns, based on their training. The analysis, described in Ambrus et al. (2019a) is comparable to the approach used in Study III of this Thesis. The neural response data on which the classifiers got trained on, are EEG responses to face images, which inherent various face features like their familiarity status, gender and identity. This process is done for each time point in the range from -200 to 1300 ms relative to stimulus onset. The outcome is a neural representational dissimilarity matrix (RDM) separate for each millisecond. To investigate the neuronal organization of face representation, the sorted data in the RDMs were matched with specific features of the faces. That was reached by first creating representational dissimilarity matrices for these conditions, in this case for identity and gender. The dissimilarity of each face-pair was modelled as a function of different predictor matrices: In the identity predictor RDM, the faces of the same identity were coded as similar and faces of different identities were coded as dissimilar. Accordingly, in the gender predictor RDM, faces of the same gender were coded as similar and faces of different gender were coded as dissimilar. Examples for both the neural, as well as the predictor RDMs are depicted in Figure 4, A & C. The second step to track representations of face identity and gender was to correlate the neural RDMs separately with the predictor RDMs. This process resulted in conclusive Spearman's correlation coefficients in a matrix, which reflected pairwise dissimilarity for each combination of faces at each time point across the epoch (Figure 4, B and D).

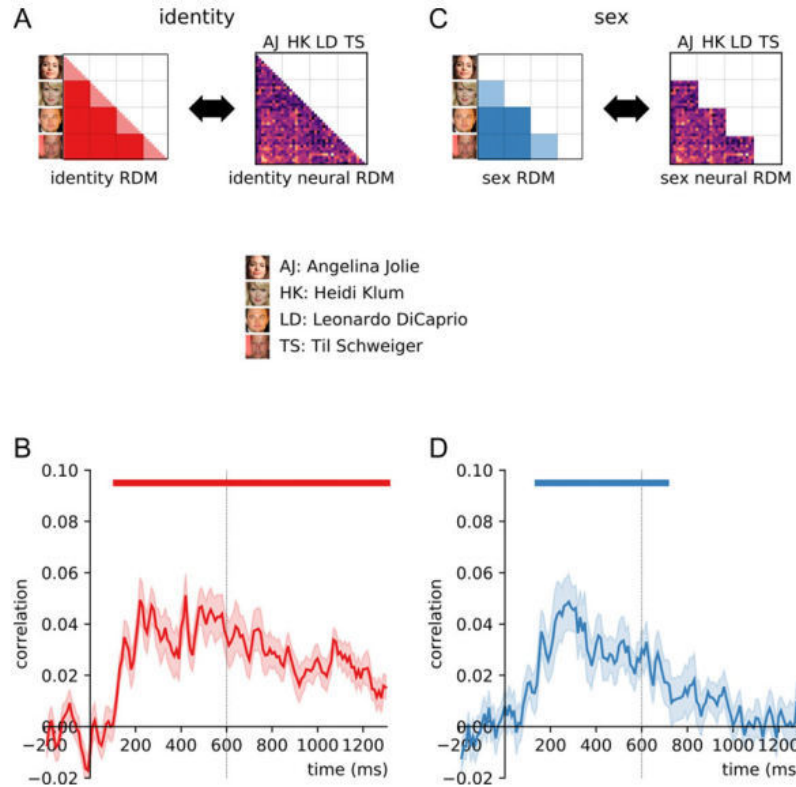


Figure 4: Examples for predictor (left) as well as neural RDMs (right) for the two face features identity (A) and gender (C) in four identities. Below, correlation coefficients matrices for both features are depicted (B, D), in which horizontal lines denote statistical significance between the predictor and neural RDM (Ambrus et al., 2019b).

The resulting correlation coefficient matrices for each face feature comprise statements about how well the trained classifiers were able to decode this feature from the neural data. Significant decoding allows the conclusion if the neural response of a specific region (e.g. occipito-temporal cortex) carries inherent information about the face feature. Hence, it can be answered if this region is involved in the processing of this feature in great temporal detail.

This method was utilized in Study III for personal, media-based and perceptual familiarity and identity correlates. The goal was to reveal familiarity as well as identity-specific representation from EEG signals to examine the process of 'getting to know' someone in great temporal detail.

3 Research Objectives

The complex temporal processing of faces described in the previous chapter 1, indicates a highly specialized system, which is in large parts unresolved in regards to familiarity and identity processing. Especially the role of the occipital face area in this task had to be revised: despite as originally described as a low-level, structural encoding area (Pitcher et al., 2007; Liu et al., 2010; Duchaine and Yovel, 2015), multiple studies attribute a more complex role to this region. Besides the involvement in learning a novel face (Ambrus et al., 2017b), the OFA is also considered necessary in identity specific processing and the association between a face and the name (Ambrus et al., 2017a, 2019a). These developments made a closer look at the OFA and its role in face learning necessary. As described previously (see 1.2 *Development of Face Familiarity*) face familiarity can be divided into several categories, depending on the involved features and modalities during face learning (personally familiar faces, famous faces, semantically familiarization via personal, semantic or episodic information, face familiarity via visual exposure) (Natu and O'Toole, 2011; Kovács, 2020).

In the four studies, described in this Thesis, we evaluated whether the OFA is causally involved in the encoding of various familiarity types. Further, linking the behavioural changes to electrophysiological evidence of the involved processes is a crucial step in deciphering the occipital-temporal cortex. Accordingly, EEG measurements were utilized in the later studies of this research strand.

To get a better understanding of the role of the occipital-temporal cortex in face familiarity and identity processing/formations, four studies were realised.

In Study I, we began by first evaluating familiarity and identity learning via visual exposure, which is achieved artificially and is therefore the least lifelike type. The familiarization with previously unfamiliar faces was reached in two levels by presenting images of a person once or 30 times. By applying TMS over the rOFA and monitoring a behavioural response, we evaluated whether the visual perceptual representations are already encoded in this region. This first study examined image-specific as well as image-independent identity representations in the rOFA.

The second Study II addressed semantic familiarity and subsequent identity representations in bilateral OFA. In this experiment, familiarization was reached by presenting personal information, a name and a job title, together with an unknown face. Even though this approach was an artificial familiarization as well, this process is ongoing in our daily routine, when learning

about a new singer or politician. Again, the causal role of the OFA in identity acquisition via semantic information was tested by applying TMS.

To include neural responses in the examination of this research question, we then implemented EEG measurements, including three learning paradigms in Study III. The first one comprised perceptual learning, the second one a media-based familiarization and the last one included personal contact to reach familiarity. The neural representations of these learning processes were analysed using RSA, as it provides a good temporal resolution of familiarity and identity correlates. This way, differential processing of faces at various levels of familiarity was evaluated over the occipital temporal cortex.

To connect the 'virtual lesion' approach using TMS with electrophysiological responses, in Study IV, we combined the stimulation of the rOFA and EEG measurements in a setup especially developed for this purpose. To test two very distinct levels of familiarity, famous celebrities were used as familiar faces. The focus of this study was the differential ERP responses elicited by familiar and unfamiliar faces as well as the evaluation if and how TMS over the rOFA influences these components.

The major research questions of the studies were the following:

I. Image-specific and -independent identity representations in the rOFA

Is the rOFA participating in the formation of image-specific and image-invariant face representations?

II. The OFAs involvement in identity acquisition via semantic information

Can we get familiarized with previous unknown faces via semantic information and is the bilateral OFA involved in this process?

III. Neural correlates of perceptual, media-based and personally known faces

What is the temporal dynamics of three different categories of familiarity and identity learning in electrophysiological responses?

IV. ERP correlates of familiar and unfamiliar faces and their modulation by stimulation of the rOFA

Can we detect the different processing of familiar and unfamiliar faces in neural ERP components and are these processes modulated by the rOFA?

4 The Present Studies

The following section includes four studies, all peer-reviewed and published or currently under review.

Study I, p. 39 ff.

I have seen you once before - evaluation of image-specific and -invariant identity representations in the occipital face area

Eick, C. M., Kovács, G., Eisele, A., Szöllősi, A., Racsmány, M., Ambrus, G. G. (2020). I have seen you once before- evaluation of image-specific and -invariant identity representations in the occipital face area. *Neuropsychologia* [under review]

Study II, p. 60 ff.

The occipital face area is causally involved in identity-related visual-semantic associations

Eick, C. M., Kovács, G., Rostalski, S. M., Röhrig, L., Ambrus, G. G. (2020). The occipital face area is causally involved in identity-related visual-semantic associations. *Brain Structure & Function* 225, pp. 1483–1493. DOI: 10.1007/s00429-020-02068-9

Study III, p. 72 ff.

Getting to know you: emerging neural representations during face familiarization

Ambrus, G. G., Eick, C. M., Kaiser, D., Kovács, G. (2020). Getting to know you: emerging neural representations during face familiarization. *The Journal of Neuroscience* [second revision]

Study IV, p. 108 ff.

Inhibition of the occipital face area modulates the electrophysiological signals of face familiarity positively: a combined cTBS-EEG study

Eick, C. M., Ambrus, G. G., Kovács, G., (2020). Inhibition of the occipital face area modulates the electrophysiological signals of face familiarity positively: a combined cTBS-EEG study. *Cortex* [submitted]

4.1 I. I have seen you once before - evaluation of image-specific and -invariant identity representations in the occipital face area

Study I

I have seen you once before - evaluation of image-specific and -invariant identity representations in the occipital face area

Eick, C. M. ^a, Kovács, G. ^a, Eisele, A. ^a, Szöllősi, A. ^{b,c}, Racsmány, M. ^{b,c}, Ambrus, G. G. ^a (2020). I have seen you once before- evaluation of image-specific and -invariant identity representations in the occipital face area. *Neuropsychologia*

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I have seen you *once* before – evaluation of image-specific and -invariant identity representations in the occipital face area

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Abstract

Identity-specific face representations are reported in the right occipital face area (rOFA), even though this region is conventionally seen as an entry point of the face processing network. Here we evaluate whether image-specific and image-invariant identity representations of ambient face images are traceable in the rOFA.

We presented face images while transcranial magnetic stimulation pulses (TMS) were applied over the rOFA during a face encoding phase of a memory task. Participants were trained on one identity with 30 different images while 30 images of different identities were presented a single time. In a subsequent retrieval phase, recognition memory was tested using a two-alternative forced-choice recognition task.

We demonstrated encoding of image-specific representations, as recognition was above chance level for the trained ID *as well as* to a lesser extent, for single-presentation images as well, independent of TMS stimulation. TMS over rOFA impaired the encoding of trained ID images. This indicates that the occipital temporal cortex, including the OFA, is involved in the encoding of image-specific face representations and emphasizes its involvement in face recognition. Further, our results suggest that the rOFA is rather involved in recollection than familiarity in recognition memory.

Keywords: Face recognition, Recognition memory, Face image processing, Transcranial magnetic stimulation, Occipital face area, Face processing network

Highlights:

- OFA is involved in the formation of image-specific face representations
- OFA is rather involved in recollection than familiarity in recognition memory
- highly variable images reinforce identity learning by building stable representations
- robust image recognition was measured after seeing a face just one time

Introduction

Familiar and unfamiliar faces seem to be processed in fundamentally different ways (Johnston & Edmonds, 2009) which may be the reason why the recognition of a familiar face is less difficult compared to less familiar identities (Megreya & Burton, 2008).

It has been argued that a critical difference between familiar and unfamiliar face recognition relates to the amount of processing based on the image-level information (Andrews et al., 2015). Getting familiarized with a face involves a generalized representation of it, such that the concept of a familiarized face becomes image-invariant. Novel faces, on the other hand, are rather processed based on a pictorial approach (Burton et al., 2011), i.e. the representation of a novel face is image-specific.

Familiarization involves seeing a person and learning more about him or her. Getting to know someone is also possible without personal interaction, simply by being exposed to videos or still images of the individual (Megreya & Burton, 2008). In experimental settings, this is achieved by presenting multiple various images of the individual (Andrews et al., 2015; Ritchie & Burton, 2017) or connecting a face to additional, non-sensory (semantic) information such as a name or a job (Eick et al., 2020; Tsukiura et al., 2010). In a recent study, involving a face-card sorting task, it has been observed that a larger number of images presented per identity improves subsequent recognition, especially if the number of identities present was known to the participants (Andrews et al., 2015). That is presumably because the exposure to an enhanced within-person image variability across luminance, orientation, and other low-level features facilitate our recognition. Even a simple average of multiple face-images within an

identity leads to a more stable face representation as the statistical mean lessens the effect of transient traits while conserving consistent aspects of the face, leading to better image-independent representations (Jenkins & Burton, 2008; Burton, A. M., Jenkins, R., Hancock, P. J., & White, D., 2005).

However, getting to know someone is not a process that reliably leads to a fixed categorical distinction (known/unknown), but it is rather a continuum between these two states (Clutterbuck & Johnston, 2002). At what point does the person you sometimes see in the supermarket gets 'familiar' i.e., when does a switch between the image-specific processing of unfamiliar faces and image-invariant processing of familiar faces occur? This question is the topic of several research programs and especially the neural correlates of familiarity remain debated (Duchaine & Yovel, 2015; Gobbini & Haxby, 2007; Haxby et al., 2000; Kovács, 2020).

Several models of face processing and recognition have been proposed in the last decades (Bruce & Young, 1986; Rapcsak, 2019). Haxby et al. (2000) introduced a two-stage network model involving a core as well as a larger, extended network. The core regions consist of the fusiform (FFA) and occipital face area (OFA), as well as the superior temporal sulcus (STS), which are involved in the early visual processing of faces. The extended system, including the anterior temporal pole (ATL), the amygdala as well as parietal and frontal areas are active in higher-level cognitive processing stages (Gobbini & Haxby, 2007; Rapcsak, 2019).

By interfering with the ongoing stimulus processing in a given area, for example by transcranial magnetic stimulation (TMS), multiple studies tested specific functions of this network. A complex interaction of all of these regions can be assumed (Ambrus et al., 2017a; Ambrus et al., 2017b; Eick et al., 2020; Atkinson & Adolphs, 2011), potentially via forward and feedback connections (Kadosh et al., 2011; Gschwind et al., 2012; Jiang et al., 2011).

The OFA is typically considered to be a relatively early, structural face processing area (Pitcher et al., 2007). However, recent studies hint towards a causal role of the OFA in 'higher' order functions as well, such as semantic information and image-invariant face processing (Eick et al., 2020; Ambrus et al., 2017a). This supports Duchaine & Yovel's (2015) revised model of face processing, based on a robust functional connection between ATL and OFA, suggesting that the OFA is more than a simple low-level, structural encoding area (Haxby et al., 2000).

Face processing is shown to be a bilateral process (Minnebusch et al., 2009), yet, the right hemisphere is the focus of the majority of studies, due to its dominance in face perception (Haxby et al., 2000; Kanwisher et al., 1997; Bentin et al., 1996; Bukowski et al., 2013). This lateralization applies to face detection in general (Gao et al., 2018) as well as to familiar face recognition (Wiese et al., 2019; Wuttke & Schweinberger, 2019). The right OFA seems to be involved in both of these processes: a lesion in the rOFA leads to impaired face discrimination capacities (Dricot et al., 2008; Schiltz et al., 2006), repetitive double-pulse TMS of the rOFA disrupts the discrimination of face parts (Pitcher et al., 2007; Pitcher et al., 2008) and the rOFA is causally involved in identity-specific processing and the learning of novel faces (Ambrus et al., 2017a; Ambrus et al., 2017b).

According to several current models, memory decisions regarding recognition are based on two separate processes: familiarity and recollection (Yonelinas, 2001; Yonelinas, 2002). Once the level of familiarity exceeds a certain criterion, participants tend to accept the stimulus as having been seen or familiar. However, in some cases, the retrieval of an item is accompanied by the sense of remembering related episodic and associated non-sensory information as well. This process, termed as recollection, refers to the situation when one retrieves a specific memory together with its contextual/episodic details. While the former (familiarity-based) decisions are presumably based on the functions of the perirhinal cortex, recollection is typically associated with the hippocampus (Brown, M. W., & Aggleton, J. P., 2001; but see Manns, J. R., Hopkins, R. O., Reed, J. M., Kitchener, E. G., & Squire, L. R. (2003) and Squire et al. (2007) for a different viewpoint).

One way to test recognition memory performance is the decision of whether subsequently presented stimuli are old items (previously seen/targets) or new stimuli (distractors). In another approach, the forced-choice recognition memory task, the target items and the distractors are presented simultaneously and the participant has to select the 'old' item. The advantage of using forced-choice recognition memory tests is a decreased impact of response bias, specifically of the tendency to say 'old' or 'new' to all stimuli. Several important factors determine the relative contribution of underlying recollection and familiarity processes in memory performance. One of these factors is the overall level of task difficulty. It has been demonstrated that when the discrimination between two presented items is difficult,

participants' decisions are based rather on recollection than on familiarity (Cook, G. I., Marsh, R. L., & Hicks, J. L., 2005).

Study objectives

To gain further insight into face identity learning and recognition memory in the ventral stream, here we test the role of the rOFA in image-invariant as well as image-specific identity encoding. Two groups of participants were shown 30 different images of one single identity (trained ID) as well as a single image of 30 other, similar-looking identities while receiving TMS over the OFA of the right hemisphere or a control area. Subsequently, they performed a two-alternative forced-choice recognition task for four different trial types containing two simultaneously presented face images. Different old and novel images were combined to evaluate identity familiarity and image familiarity, each in an easy and a difficult task, separately.

The aim of this study is twofold: (1) As previous studies found that the OFA is involved in identity learning (Ambrus et al., 2017a; Eick et al., 2020; Ambrus et al., 2017b), the current experiment tests whether identity and image familiarity are affected by TMS over rOFA similarly. Hence, the conclusion if the occipito-temporal network, including the OFA, is causally involved in creating a) image-invariant and b) image-specific identity representation from individual images will be possible. (2) Additionally, we test if the exposure to 30 naturally variable images of a given identity creates a more stable image representation than a single exposure to a given face.

Methods

Participants

Forty right-handed participants with normal or corrected to normal vision and no prior psychological or neurological conditions were measured in the course of the study. They had no metal implants and reported no regular medication intake, relevant to the study. The experimental group of 20 participants (age (mean \pm SD) of 23.5 years (3.2); male = 2) received TMS over the right OFA while another group of 20 randomly selected participant (age of 21.1 years (3.1); male = 2) was stimulated over Cz as a control site. The sample size was based on prior TMS studies of the laboratory (Eick et al., 2020; Ambrus et al., 2017a; Ambrus et al.,

2017b). All participants received compensation (monetary/ partial course-credits). Prior to the experiment, the written consent of all participants was obtained. The study was approved by the ethics committee of the University of Jena and the guidelines of the Declaration of Helsinki were observed.

Functional localization and transcranial magnetic stimulation of right OFA

Functional neuroimaging data of each participant was collected to localize the right OFA (Siemens MAGNETOM Prisma fit, Erlangen, Germany; Institute for Diagnostic and Interventional Radiology, University of Jena). High-resolution sagittal T1-weighted images were obtained using a magnetization EPI sequence for 3D head and brain meshes (MP-RAGE; TR = 2300 ms; TE = 3.03 ms; 1 mm isotropic voxel size). For the functional MRI images, a 20-channel phased array head-coil and a gradient-echo, T2-weighted EPI sequence was used (35 slices, 10° tilted relative to axial, TR = 2000 ms; TE = 30 ms; flip angle = 90°; 64 × 64 matrices; 3 mm isotropic voxel size). During the functional scanning, a standard localizer run was administered, including 20 s epochs of faces, objects, and Fourier-randomized versions of faces, interleaved with 10 s rest periods. With a stimulus presentation frequency of 2 Hz (300 ms exposition time and a 200 ms inter-stimulus interval) the localizer was 640 s long and presented in Matlab (MathWorks, Version R2013; (Amado et al., 2016).

Pre-processing and statistical analysis were conducted using SPM12 (Wellcome Department of Imaging Neuroscience, London, UK, Version 12) in Matlab. The locations of the rOFA were determined individually (threshold of $p < 0.001_{\text{uncorr.}}$, contrasting t-maps of faces vs. Fourier-randomized faces and objects; for details see Cziraki et al. (2010)). The mean (\pm SD) MNI coordinates for the rOFA ($n = 20$) were 41.1 (1.1), -77.3 (1.9), 11.1 (0.9), and their locations on an average brain are depicted in Fig. 1.

The rOFA or the control area Cz were stimulated with a PowerMag 100 Research Stimulator (MES Forschungssysteme GmbH) and the appropriate neuronavigational system PowerMag View (MES Medizintechnik GmbH) was used to help the identification of the target areas. Three single-pulses per image (100 ms prior, concurrent with, and 100 ms after image onset) were delivered during the encoding phase of the experiment (see below). The intensity of the stimulation was set to 65% of the maximum stimulator output (Silvanto et al., 2017; Silvanto & Cattaneo, 2017a).

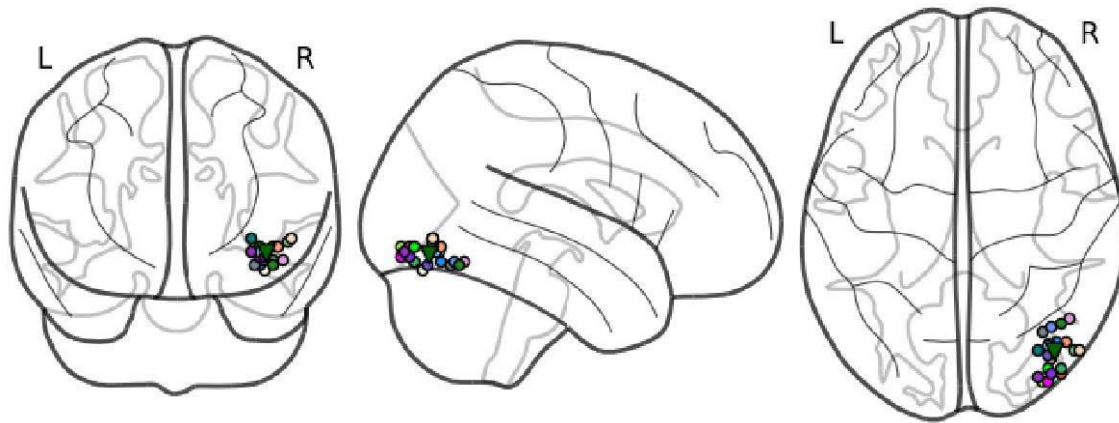


Figure 1 The location of the transcranial magnetic stimulation over the right occipital face area for the 20 participants in the stimulation group (colored dots), as well as the average position of rOFA across the participants (green triangle).

Stimuli

Faces of 76 female identities were selected from an in-house database, depicting similar-looking, unfamiliar individuals (greyscale ambient portraits with neutral or positive facial expressions). One person served as the training identity (trained ID); 60 images of her were collected, of which 30 were used as training images. To ensure that all images of the 75 unfamiliar IDs and all the 60 images of the trained ID had the same level of variation and did not differ in low-level features, pixel-similarity and structural dissimilarity matrixes were calculated for all three groups (creating a Pearson correlation coefficient (PCC) and a structural similarity index (SSI) respectively of the comparison of each image with all others) (Wang, Z., Bovik, A. C., Sheikh, H. R., & Simoncelli, E. P., 2004). The resulting mean values of PCC and SSI were 0.31/0.26 for all images, 0.27/0.26 within the 75 different ID images, and 0.32/0.26 within the 60 images of the trained ID (1 = high similarity; 0 = low similarity), suggesting a similar variance across all included images. The images had a size of $6.23^{\circ} \times 8.54^{\circ}$ visual angle (BenQ LED display at 1680×1050 pixel resolution and refresh rate of 60 Hz) and were presented on a uniform gray background at a viewing distance of 60 cm. The experimental software was written in PsychoPy (Peirce, 2007).

Experimental procedure

During the encoding phase (Fig. 2a), each of the 30 images of the trained ID and 30 images of the other IDs (single-presentation images) were presented once in a randomized order. The presentation time was 300 ms, the interstimulus interval (ISI) was 200 ms. A fixation cross was

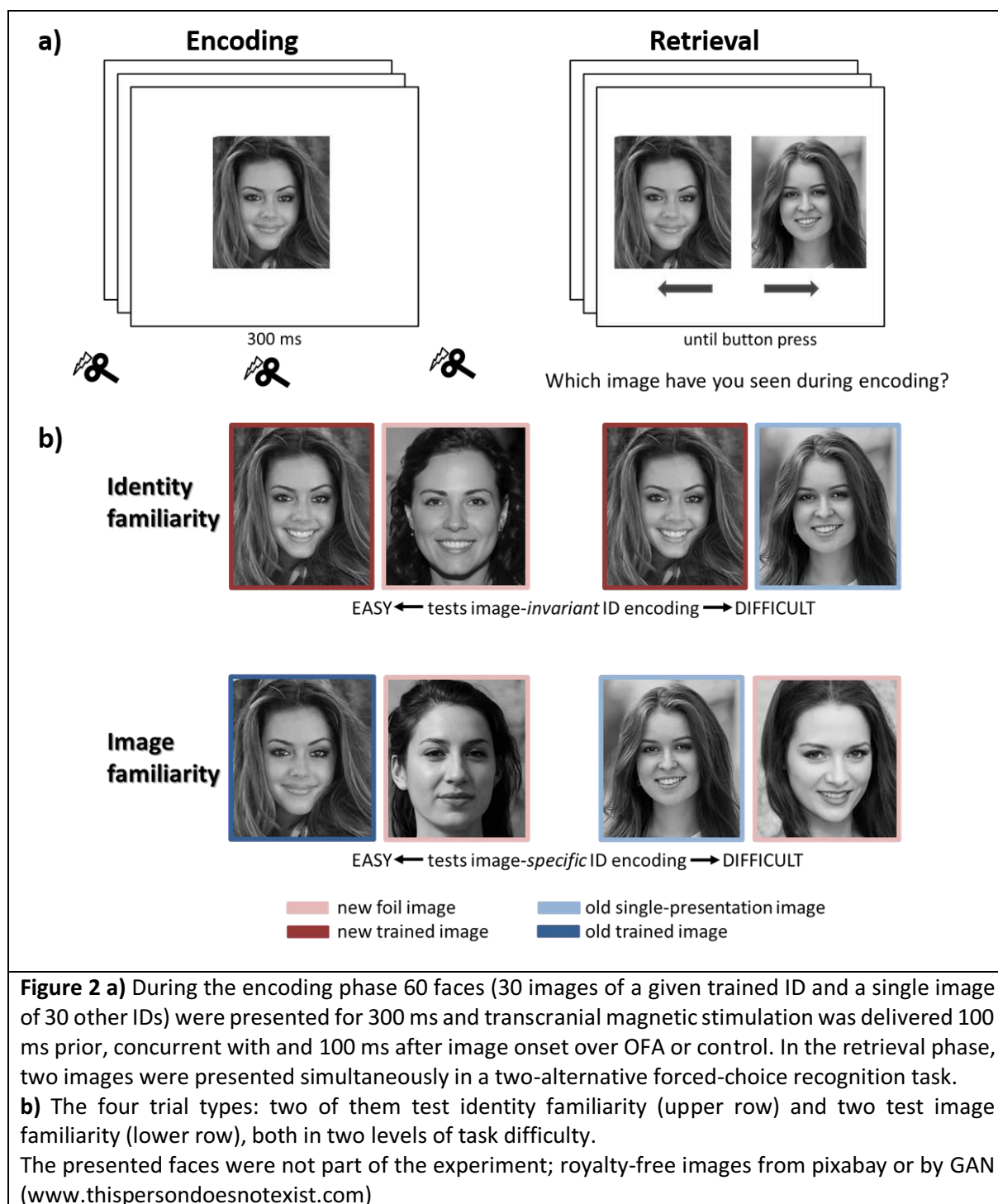
shown in the beginning and between the trials. The participants were instructed to memorize the images (not the identities depicted, “Please be attentive and try to remember the following images”). The 30 images of the trained ID and the single-presentation images, presented during this phase, served as *old* items in the subsequent phase.

The retrieval phase (Fig. 2a) was performed immediately after the completion of the encoding phase. In each trial, two images were presented together with randomized left-right positions until a button press. The ISI with a fixation cross was 500 ms. Participants were required to select the image they thought to have seen during the encoding phase (‘old image’) by pressing the right or left arrow key. Technically, the task was a two-alternative forced-choice recognition paradigm in which three conditions contained images related to the encoding phase paired with a hereto unseen image of an unfamiliar face (foil image), while in one condition a novel trained ID image was paired with an old single-presentation image.

Altogether four different trial types were presented. Two trial types with different levels of task difficulty tested *identity familiarity* of the trained ID (Fig. 2b). In the easy trial type, a new image of the trained ID was paired with a foil image. In the difficult trial type, a new trained ID image was presented together with a single-presentation image. In these trial types, the trained ID is known but the presented new image is not, hence *image-invariant* ID encoding is tested. We report the participant’s performance of how often a new image of the trained ID was endorsed as old. If a tendency towards this response is observed, it indicates a response bias due to identity familiarity. We term this tendency *familiarity bias*.

The two other trial types tested *image familiarity* (Fig. 2b), again, in two levels of task difficulty. In the easy trial type, an old image of the trained ID was presented together with a foil image. In the difficult trial type, an old single-presentation image was paired with a foil image. We report the participant’s performance of how often an old image was recognized as old, which tests *image-specific* ID encoding.

In total the experiment took 20 minutes and 60 trials (15 trials in four trial types) were presented for each stimulation condition.



240

241 Statistical analysis

242 To evaluate the two trial types testing *identity familiarity*, the performance of endorsing a
 243 trained ID as old was analyzed with a mixed ANOVA (between-subject factor: *TMS* (OFA,
 244 Control); within-subject factor: *Trial Type* (easy, difficult)). We examined whether the
 245 stimulation of rOFA influences the response bias towards the new image of the trained ID.

The two trial types testing *image familiarity* were analyzed by evaluating the accuracy of correctly selected old images in another mixed ANOVA (between-subject factor: *TMS* (OFA, Control); within-subject factor: *Trial Type* (easy, difficult)). If stimulation over the rOFA changed the performance of correctly identifying previously seen images as old was evaluated as well.

Additionally, all performances were tested against the chance level of 50% using a one-sample t-test.

Results

Identity familiarity was evaluated in two trial types, in an easy and a difficult task. New images of the trained ID were more frequently endorsed as old in both. However, the performance was different between the two trial types (Fig. 3; main effect of *Trial Type*: $F(1,38) = 28.41$, $p < .000$, $\eta^2_p = .428$): participants endorsed novel images of the trained ID as old significantly more frequently in the easy trial type (mean = 80%), when compared to the difficult trial type (mean = 66.6%). This suggests that the false endorsement of new trained ID images as old against a foil image was easier than the one against a single-presentation image, that has been seen before. Although there was no influence of TMS on the overall performance (main effect of *TMS*: $F(1,38) = 1.81$, $p = .186$, $\eta^2_p = .046$), a Sidak corrected post-hoc test revealed that TMS influenced the choice in the difficult trial type between new images of the trained ID and old single-presentation images (at $p = .035$). The rOFA stimulation group endorsed new images of the trained ID more often as old when compared to the control group, (rOFA stim. = 70.33%, Cz stim. = 63%). Stimulation of the rOFA in the encoding phase impaired the encoding of the trained ID images, which suggests the involvement of the rOFA in image-specific face learning and recognition. There was no interaction between the two factors (*Trial Type***TMS*: $F(1,38) = 1.78$, $p = .191$, $\eta^2_p = .045$) and all performances were above the 50% chance level (all $p < .000$).

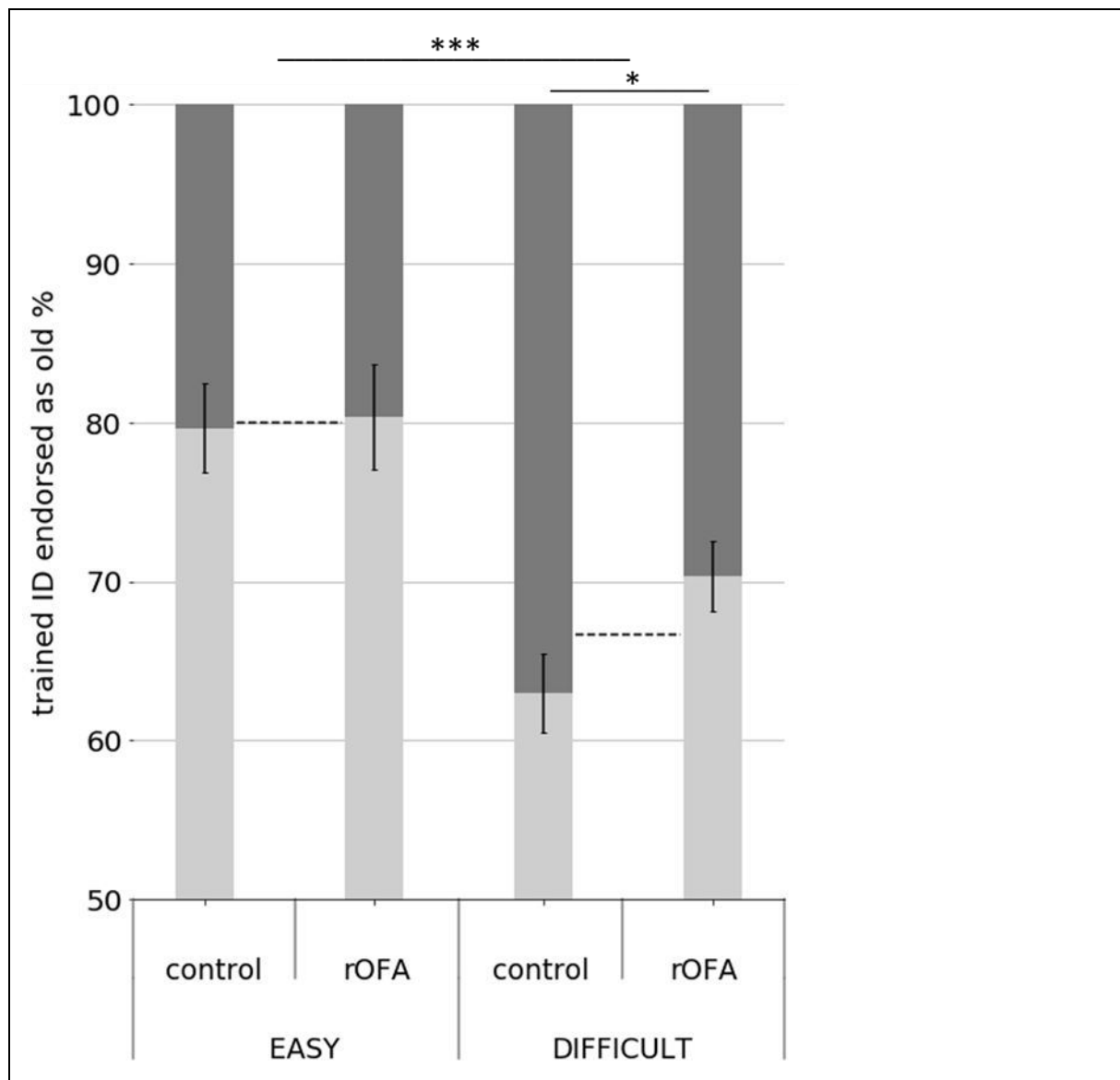


Figure 3 Identity familiarity: Percentage of new images of the trained ID endorsed as old (light grey bars) after rOFA and control stimulation in the two trial types testing image-invariant ID encoding (EASY: new trained ID image vs. foil image; DIFFICULT: new trained ID image vs. single-presentation image). Dark grey bars indicate the choice of the other presented image as old (*mean ± SE*; *** $p \leq .001$, * $p \leq .05$; --- mean of the trial type (control + rOFA)).

273

274 Image familiarity was also evaluated in two trial types, in an easy and a difficult task. In both
 275 trial types, regardless of whether an identity was previously seen 30 times or only once, old
 276 images were correctly recognized as old against foil images in more than 50% of cases (all $ps <$
 277 .001). This suggests, that seeing 30 images of a person, but also seeing a face only once is
 278 sufficient to encode and recognize it, at least in the short time interval after the initial
 279 exposure in our experiment. The performance, as expected, was significantly better for
 280 recognizing images of the trained ID (mean = 82.8%) compared to the single-presentation

images, showing an advantage of multiple image presentations (mean = 63%; Fig. 4; main effect of *Trial Type*: $F(1,38) = 43.15$, $p < .000$, $\eta^2_p = .532$). Again, there was no influence of TMS on performance (main effect of *TMS*: $F(1,38) = .00$, $p = .959$, $\eta^2_p = .000$) and neither an interaction was observed between the factors (*Trial Type***TMS*: $F(1,38) = .15$, $p = .701$, $\eta^2_p = .004$).

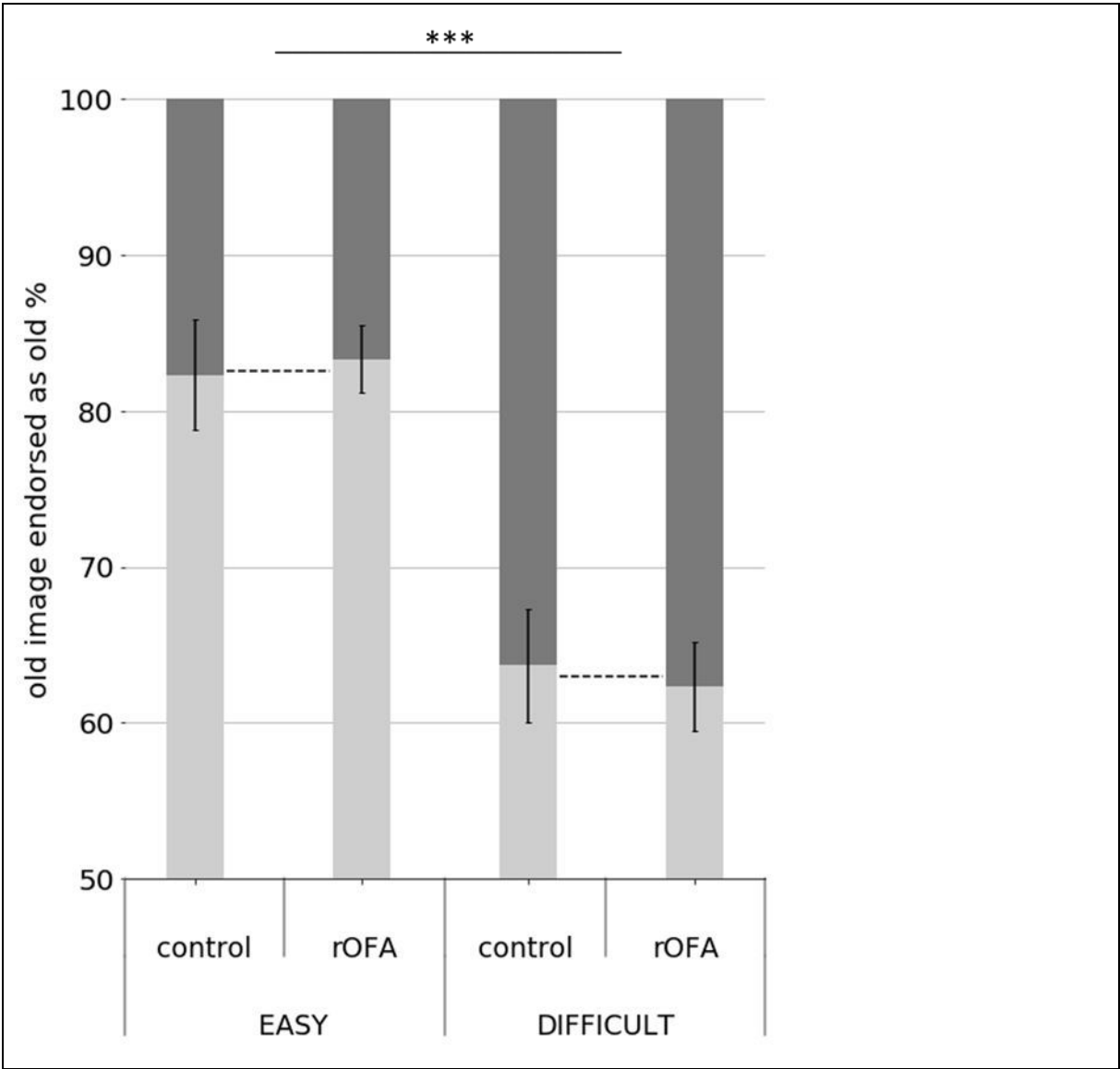


Figure 4 *Image familiarity*: Percentage of old images endorsed as old (light grey bars) after rOFA and control stimulation in the trial types testing image-specific ID encoding (EASY: old trained ID image vs. foil image; DIFFICULT: single-presentation image vs. foil image). Dark grey bars indicate the choice of the other presented image as old (*mean ± SE*; *** $p \leq .001$; --- *mean of the trial type (control + rOFA)*).

Overall, these results suggest that the stimulation of the rOFA interferes with image-specific face encoding and that the current paradigm leads to the engagement of recognition memory processes after a single exposure as well as after training with 30 images.

Discussion

We evaluated the role of the right OFA in image-invariant as well as image-specific identity encoding, using neuronavigated transcranial magnetic stimulation. TMS was applied during face image encoding while recognition memory was tested subsequently in a two-alternative forced-choice recognition task.

The major results of the experiment are the following: (1) TMS of rOFA interferes with image-specific face encoding and therefore impairing identity familiarity decisions. This suggests that the rOFA, presumably in interplay with other face-sensitive areas, is of importance for face image learning and recognition. (2) The emergence of a stable face identity representation can be demonstrated both after presenting several different images of a person, but also, to a lesser degree when a single face image is presented once. The implications of these results are discussed below.

Identity familiarity: Stimulation of rOFA facilitates a familiarity bias

The main outcome of this study is that the rOFA is involved in creating image-specific face representations, evident in a reduced differentiation between old and new images of the trained ID.

In the difficult trial type of the condition testing identity familiarity, a new image of the trained ID was presented together with an image that has been seen once during the encoding phase (single-presentation image). We observed a response bias towards the false endorsement of the new image of the trained ID as old. This tendency is an indication of familiarity towards the trained ID, hence a familiarity bias. Interestingly, we found a significantly larger familiarity bias in the group receiving TMS over the rOFA when compared to Cz. In that group, participants chose the new image of the trained ID as old more frequently (70%), compared to the control group (63%), suggesting that the stimulation of rOFA enhances this familiarity bias.

If we assume that this region is involved in identity-specific processing and the learning of novel faces the question arises why this familiarity bias is enhanced and not reduced after

stimulation of the rOFA. Answering this question requires a look at the task which was to indicate the 'old' image seen during the encoding phase: After stimulation of the rOFA, participants more frequently chose the 'wrong' answer by selecting the new image of the trained ID as old. The reason for that behavior could be that the encoding of the images of the trained ID was impaired by TMS over the rOFA. The control group, on the other hand, was able to encode the images of the trained ID without interference and were, therefore, better able to distinguish them from new images of the same person later during the retrieval phase. Thus, the OFA is crucial for encoding image-specific face representations and differentiating them from other images.

Further, TMS over the rOFA impacted only this difficult trial type testing identity familiarity (the decision between a new image of the trained ID and a single-presentation image). As the trained ID is known but the presented new image is not this condition tests image-invariant ID encoding. However, the other presented item, the single-presentation image that has been seen once before, tested image-specific ID encoding. Hence, only this trial type combined the retrieval of image-invariant as well as image-specific ID encoding. As this trial type was affected by TMS over the rOFA, it suggests that this region is involved in the differential processing of image-invariant (new trained ID) and image-specific ID memory traces (IDs seen once). To conclude, the right OFA is involved in the encoding of an image-specific face representation as well as differentiating it from image-invariant ID representations.

One reason why we do not observe a TMS effect in the easy trial type of the condition testing identity familiarity might relate to the fact that there is no interference between image-invariant and image-specific ID encoding. Only image-invariant ID representation was tested by presenting a new image of the trained ID together with a foil image. Hence, TMS of the rOFA could not impair interference resolution, as there was no interference in the test situation. Additionally, in the easy trial type, there was no 'correct' answer to the question, which image was old, as participants have neither seen the foil images nor the new images of the trained ID. Endorsing the trained ID images as old was the more intuitive choice even if the participants might have been aware of the incorrectness of their answers.

The outcome of this study reveals the involvement of the OFA not only in identity learning as found in previous studies (Ambrus et al., 2017a; Ambrus et al., 2017b; Eick et al., 2020) but also in image-specific face ID encoding.

Image familiarity: Image recognition even after a single exposure

Our second major result is that the current paradigm can establish image memories for an identity presented with multiple exemplars, and, to a lesser extent, this is also possible for single-exposure identities.

The results in the trial types testing image familiarity reveal image-specific ID encoding, both for the old images of the trained ID and for old single-exposure images. Participants chose these old images significantly more often (82%/ 63%) than the foil images. The performance of recognizing old trained images is significantly higher compared to the recognition of single-presentation images, which most likely reflects image-based encoding as well as identity learning of the trained ID. Getting to know someone is a continuous process and modelling it using this paradigm only allows for a limited interpretation as we exposed our participants to a set of 30 images of the trained ID. However, it is interesting that following only a single presentation, the image is reliably recognized above the chance level.

Testing familiar faces is a common practice in face research but the process of getting 'familiarized' is still heavily discussed as it is not yet resolved entirely (Goesaert & Beeck, 2013; Andrews et al., 2015; Clutterbuck & Johnston, 2002; Kovács, 2020). In a study similar to ours, Ritchie & Burton (2017) tested facial identity learning from variable images. Previously unfamiliar faces were learned with photos of high (taken at different occasions) or low (video stills from one video) variability and participants had to complete a name-face matching task or a same-different face-matching task. In all cases, accuracy was higher for faces learned in the high variability condition and performance did not depend on whether the test image was from the high or low variability batch (Ritchie & Burton, 2017). As expected, our study demonstrates similar results, as the faces seen with high variability (30 images) lead to a higher recognition performance than faces without variability (seen once). By controlling image variability instead of treating it as unwanted noise, one can either achieve a more life-like stimuli set to evaluate facial recognition with high variability (Young & Burton, 2017) or focusing on a pictorial memory test with more controlled images (low variability; Burton et al., 2011).

Impact on image memory

One important feature of episodic memory is the ability to encode and store information in the form of unique memory representations (Tulving, 1972). Strongly related to episodic

memory is the ability to decrease the overlap among memory representations that share similar features (Hunsaker & Kesner, 2013; Yassa & Stark, 2011).

We tested identity familiarity with a difficult trial type, in which participants were required to differentiate between a new image of the trained ID and a single-presentation image. Stimulation of the rOFA decreased the endorsement rate (chosen as old) when interference resolution was needed. In this case, we assume interference with the trained ID recognition, because the old, single-presentation images, were also familiar, as discussed above, even after just one previous exposure.

In addition to other factors, the level of difficulty determines the contribution of underlying processes (recollection and familiarity) in the memory performance. The more difficult a discrimination task is, the participants' decisions are rather based on recollection than on familiarity (Cook, G. I., Marsh, R. L., & Hicks, J. L., 2005). Hence, as the decision between a new image of the trained ID and a single-presentation image is challenging due to an increase in interference, the performance probably relies more on recollection, in contrast to familiarity. This would lead to another conclusion regarding the role of the OFA in this task. As a stimulation effect was only evident in this trial type, it might hint at a modulatory effect on the underlying recognition memory processes, suggesting that the occipital temporal lobe, including the OFA, is rather involved in recollection than familiarity. To address the association between specific areas in the face-network and memory processes, such as familiarity and recollection, further research is required.

Impact on the models of face processing

The results of this study are in line with previous experiments regarding the role of OFA in face processing. Previous TMS studies reported the involvement of the OFA in identity-dependent face processing and thereby questioning the strict hierarchical feed-forward models of face processing (Ambrus et al., 2017a; Ambrus et al., 2017b; Eick et al., 2020). This study further explores the involvement of the OFA in these functions. Despite being involved in identity processing and connecting semantic information to novel faces, our study demonstrates that the right OFA also plays a causal role in image-specific face learning and recognition. This finding is in line with previous studies, which report no change in familiarity decision tasks after image priming during TMS of rOFA (Ambrus et al., 2017a). As state-dependent TMS is assumed to facilitate the less excitable neural populations, image-specific ID encoding can be

assumed (Silvanto & Cattaneo, 2017b). Further, our results suggest, that the right OFA is involved in the differentiation between image-specific and image-invariant ID representations, which may rely on higher face processing steps. This wide range of roles of the OFA emphasizes its crucial involvement in face recognition per se and hints towards a well-connected interaction of the whole face processing network.

Conclusion

By presenting ambient face images of a person once *or* 30 times, and a subsequent two-alternative forced-choice recognition memory task, this study tested image familiarity and identity familiarity. Stimulation of the rOFA during encoding revealed that the OFA is involved in encoding image-specific face representations and differentiating these from other presented images. Additionally, the evaluation of recognition memory suggests that the rOFA is rather involved in recollection than familiarity per se.

Robust immediate recognition of an image could be measured after seeing a face 30 times but, to a lesser extent, after a single exposure as well. This can be seen as the first step towards the emergence of familiarity information and it further suggests that multiple variable images support identity learning and encoding a representation of a face (Ritchie & Burton, 2017).

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Conflict of interest: The authors declare that they have no conflict of interest.

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4.2 II. The occipital face area is causally involved in identity-related visual-semantic associations

Study II

The occipital face area is causally involved in identity-related visual-semantic associations

Eick, C. M. ^a, Kovács, G. ^a, Rostalski, S. M. ^a, Röhrig, L. ^a, Ambrus, G. G. ^a (2020). The occipital face area is causally involved in identity-related visual-semantic associations. *Brain Structure & Function* 225, pp. 1483–1493. DOI: 10.1007/s00429-020-02068-9

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The occipital face area is causally involved in identity-related visual-semantic associations

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Abstract

Faces are processed in a network of areas within regions of the ventral visual stream. However, familiar faces typically are characterized by additional associated information, such as episodic memories or semantic biographical information as well. The acquisition of such non-sensory, identity-specific knowledge plays a crucial role in our ability to recognize and identify someone we know. The occipital face area (OFA), an early part of the core face-processing network, is recently found to be involved in the formation of identity-specific memory traces but it is currently unclear if this role is limited to unimodal visual information. The current experiments used transcranial magnetic stimulation (TMS) to test whether the OFA is involved in the association of a face with identity-specific semantic information, such as the name or job title of a person. We applied an identity-learning task where unfamiliar faces were presented together with a name and a job title in the first encoding phase. Simultaneously, TMS pulses were applied either to the left or right OFA or to Cz, as a control. In the subsequent retrieval phase, the previously seen faces were presented either with two names or with two job titles and the task of the participants was to select the semantic information previously learned. We found that the stimulation of the right or left OFA reduced subsequent retrieval performance for the face-associated job titles. This suggests a causal role of the OFA in the association of faces and related semantic information. Furthermore, in contrast to prior findings, we did not observe hemispherical differences of the TMS intervention, suggesting a similar role of the left and right OFAs in the formation of the visual-semantic associations. Our results suggest the necessity to reconsider the hierarchical face-perception models and support the distributed and recurrent models.

Keywords Semantic face processing · Transcranial magnetic stimulation · Occipital face area · Face processing network · Semantic information · Recognition

Introduction

Faces are processed in regions along the ventral object vision pathway (Ungerleider and Haxby 1994). However, face processing deviates from object or body processing, as faces also carry conceptual knowledge of the person (Lambon Ralph et al. 2009; Pitcher et al. 2009). The recognition of a person involves the process of identifying the face as well as learning and recalling the associated person-related knowledge, such as a name, associated and relevant places or the occupation a person. The first influential cognitive model

of face recognition by Bruce and Young (1986) considered the two functional components of ‘recognizing a face’ and that of ‘encoding the relevant identity-specific semantic information’ to be inseparable. Addressing the criticism that these models assumed the existence of a single “face recognition unit” and were not based on neurophysiological data, Haxby et al. (2000) further developed the model into a neuronally motivated, two-stage network model. The core of this model, comprising the fusiform (FFA) and occipital face areas (OFA) as well as the superior temporal sulcus (STS), is involved in the early visual processing of faces. The extended system, on the other hand, including the anterior temporal pole (ATL), the amygdala, parietal as well as frontal areas (Gobbini and Haxby 2007; Rapcsak 2019), is active in higher-level cognitive processing such as semantic knowledge, emotional and motivational evaluation as well

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4.3 III. Getting to know you: emerging neural representations during face familiarization

Study III

Getting to know you: emerging neural representations during face familiarization

Ambrus, G. G. ^a, Eick, C. M. ^a, Kaiser, D. ^b, Kovács, G. ^a (2020). Getting to know you: emerging neural representations during face familiarization. *The Journal of Neuroscience*

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Getting to Know You: Emerging Neural Representations during Face Familiarization

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The successful recognition of familiar persons is critical for social interactions. Despite extensive research on the neural representations of familiar faces, we know little about how such representations unfold as someone becomes familiar. In three EEG experiments on human participants of both sexes, we elucidated how representations of face familiarity and identity emerge from different qualities of familiarization: brief perceptual exposure (Experiment 1), extensive media familiarization (Experiment 2), and real-life personal familiarization (Experiment 3). Time-resolved representational similarity analysis revealed that familiarization quality has a profound impact on representations of face familiarity: they were strongly visible after personal familiarization, weaker after media familiarization, and absent after perceptual familiarization. Across all experiments, we found no enhancement of face identity representation, suggesting that familiarity and identity representations emerge independently during face familiarization. Our results emphasize the importance of extensive, real-life familiarization for the emergence of robust face familiarity representations, constraining models of face perception and recognition memory.

Key words: EEG; familiarity; identification; multivariate pattern analysis; person recognition

Significance Statement

Despite extensive research on the neural representations of familiar faces, we know little about how such representations unfold as someone becomes familiar. To elucidate how face representations change as we get familiar with someone, we conducted three EEG experiments where we used brief perceptual exposure, extensive media familiarization, or real-life personal familiarization. Using multivariate representational similarity analysis, we demonstrate that the method of familiarization has a profound impact on face representations, and emphasize the importance of real-life familiarization. Additionally, familiarization shapes representations of face familiarity and identity differently: as we get to know someone, familiarity signals seem to appear before the formation of identity representations.

Introduction

Across our lifetimes, we continuously become familiar with new faces. Being able to recognize familiar people is critical for social interactions. Determining the facial identity of a person, however, is a computationally challenging endeavor. This is because every face shares the same basic features; thus, telling the faces of different people apart is difficult (for review, see Peterson and Rhodes, 2006). Further, the facial features of an individual show

enormous variability across time because of illumination, viewpoint, facial expression, hairstyle, makeup, and age changes, thereby also making the task of “telling people together” very difficult (Jenkins et al., 2011; Andrews et al., 2015). Given these difficulties, it is not surprising that special brain mechanisms have developed for the identification of familiar faces (Haxby et al., 2000; Calder and Young, 2005; Gobbini and Haxby, 2006, 2007; Duchaine and Yovel, 2015; Ramon and Gobbini, 2018; Young and Burton, 2018; Rapcsak, 2019). Recent studies investigating the temporal dynamics of face processing suggested that both earlier, feedforward and later, feedback processes are important for identification (Visconti di Oleggio Castello and Gobbini, 2015; Dobs et al., 2019; Wiese et al., 2019). Cortical processing differs between different face identities within the first 200 ms, for both unfamiliar (Nemrodov et al., 2016, 2018; Vida et al., 2017) and familiar faces (Ambrus et al., 2019; Dobs et al., 2019). However, the earliest representations of facial identity seem to be explained by visual features shared between people, whereas later representations (from

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4.4 IV. Inhibition of the occipital face area modulates the electrophysiological signals of face familiarity positively: a combined cTBS-EEG study

Study IV

Inhibition of the occipital face area modulates the electrophysiological signals of face familiarity positively: a combined cTBS-EEG study

Eick, C. M. ^a, Ambrus, G. G. ^a, Kovács, G. ^a, (2020). Inhibition of the occipital face area modulates the electrophysiological signals of face familiarity positively: a combined cTBS-EEG study. *Cortex*

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Research Report

Inhibition of the occipital face area modulates the electrophysiological signals of face familiarity: A combined cTBS-EEG study

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Occipital face area

ABSTRACT

The occipital face area (OFA) is hierarchically one of the first stages of the face processing network. It has originally been thought to be involved in early, structural processing steps, but currently more and more studies challenge this view and propose that it also takes part in higher level face processing, such as identification and recognition. Here we tested whether the OFA is involved in the initial steps of recognition memory and plays a causal role in the differential processing of familiar and unfamiliar faces. We used an offline, inhibitory continuous theta-burst stimulation (cTBS) protocol over the right OFA and the vertex as control site. Electroencephalographic (EEG) recording of event-related potentials (ERPs), elicited by visually presented familiar (famous) and unfamiliar faces was performed before and after stimulation. We observed a difference in ERPs for famous and unfamiliar faces in a time-window corresponding to the N250 component. Importantly, this difference was significantly increased by cTBS of the right OFA, suggesting its causal role in the differential processing of familiar and unfamiliar faces. The enhancement occurred focally, at electrodes close to the right hemispheric cTBS site, as well as over similar occipito-temporal sites of the contralateral hemisphere. To the best of our knowledge, this is the first study showing the causal role of the rOFA in the differential processing of familiar and unfamiliar faces, using combined cTBS and EEG recording methods. These results are discussed with respect to the nature of familiar face representations, supported by an extensive, bilateral network.

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5 Discussion

The occipital face areal was previously described as a low-level entry point of the face network (Pitcher et al., 2007; Liu et al., 2010; Duchaine and Yovel, 2015). In the course of this Thesis, we evaluate this statement in three studies (I, II & IV) with a focus on identity and familiarity representations. Further, the temporal development of familiarity was investigated (Study III & IV). The next paragraph summarizes the included studies and repeats the most crucial outcome, for which Figure 29 (p. 138) serves as an overview.

Study I (4.1) focused on **image-specific and image-invariant identity representations** of ambient images in the rOFA. Behaviourally, image-specific encoding was evaluated by the recognition performance of previously seen images; image-invariant representations were determined by the recognition of new images of a trained identity. Results indicate, that the encoding of image-specific face representations is impaired by TMS over the rOFA. The incorrect choice of selecting new images as seen before (old) was enhanced and the correct identification of old images, based on their image-specific representations, was reduced (Fig. 7, p. 50 [11]). However, this effect is only visible in the decision (a two-alternative forced-choice task) involving interference between image-invariant and image-specific representations. Hence, this hints towards a causal involvement of the rOFA in the differentiation between image-specific and image-invariant face representations.

After this outcome showed, that the role of the OFA in face processing includes an even wider range than previously reported, we wanted to examine its involvement in a familiarity level associated with higher processing steps. *Study II* (4.2) accordingly tested **identity related visual semantic associations** and if they are formed with the involvement of the right and left OFA. That was reached by applying an identity-learning task, in which an unfamiliar face was encoded together with two semantic information about this face. The stimulation of the right, as well as the left OFA, reduced subsequent retrieval performance for the face-associated job titles, which suggests a causal role of the OFA in semantic knowledge retrieval (Fig. 11, p. 66 [1488]). As this function has been related exclusively to higher face processing in the extended system of the face network (Chiou and Lambon Ralph, 2018; Rice et al., 2018; Tsukiura et al., 2010), the outcome rather supports distributed and recurrent models of face processing.

As the influence of the OFA in the development of **face familiarity and identity** becomes more apparent, we then connected their emergence with **cortical activity over occipital-temporal regions**. Hence, in *Study III* (4.3), we developed three experiments with different types of face

familiarization and evaluated their neural representations. The levels of familiarity have been reached by perceptual (Experiment 1) and media exposure (Experiment 2) as well as real-life personal meetings (Experiment 3). Before and after the familiarization process, EEG has been measured during the presentation of the familiarized as well as unfamiliar faces. The following time-resolved RSA in the posterior electrode cluster depicted a clear image about how the familiarization quality influences representations of a face: Neural representation of face familiarity was not decodable after perceptual familiarization, however after familiarization via media exposure (watching a series) traces were significant at a time range around 400 to 510 ms (post-stimulus onset) in the left hemisphere only. The personal familiarization left the greatest impression, as familiarity decoding could be shown 440 to 1050 ms in the left and 420 to 790 and 880 to 990 ms in the right posterior hemisphere (Fig. 13, p. 79 [7]). The evaluation of identity representations (separately for familiarized and unfamiliar faces) however, did not convey a clear outcome. Identity formations were comparable between familiar and unfamiliar faces, as well as between the pre and post measurements. Also, the three familiarization strategies did not alter identity representations, as all showed evident patterns around 200 ms (Fig. 14, p. 80 [8]). The early onset rather hints towards perceptual differences due to the identities' visual features and not genuine identity representation due to semantic and contextual background.

To connect **neural responses to faces and their familiarity status over the occipital-temporal cortex with functions of the rOFA**, in *Study IV* (4.4) we developed a setup to combine the methods EEG and TMS. To secure clear and differentiable familiarity components, we showed already familiar (famous) and completely unfamiliar faces during two EEG measurements, the first prior to and the second directly after cTBS over the rOFA (and a control region). First, a familiarity effect was visible in the N250 ERP component of the pre measurements in electrodes located over the occipital-temporal cortex (Fig. 27, p. 119 [11]). Second, this effect bilaterally increased after stimulation of the rOFA, due to enhanced amplitudes in the familiar face response (Fig. 28, p. 121 [13]). This facilitation points towards a cTBS induced modulation on inhibitory connections of the rOFA on other cortical sites. Additionally to the causal role of the rOFA in the differential processing of famous and unfamiliar faces, the bilateral effects show a closely cooperating inter-hemispherical connection.

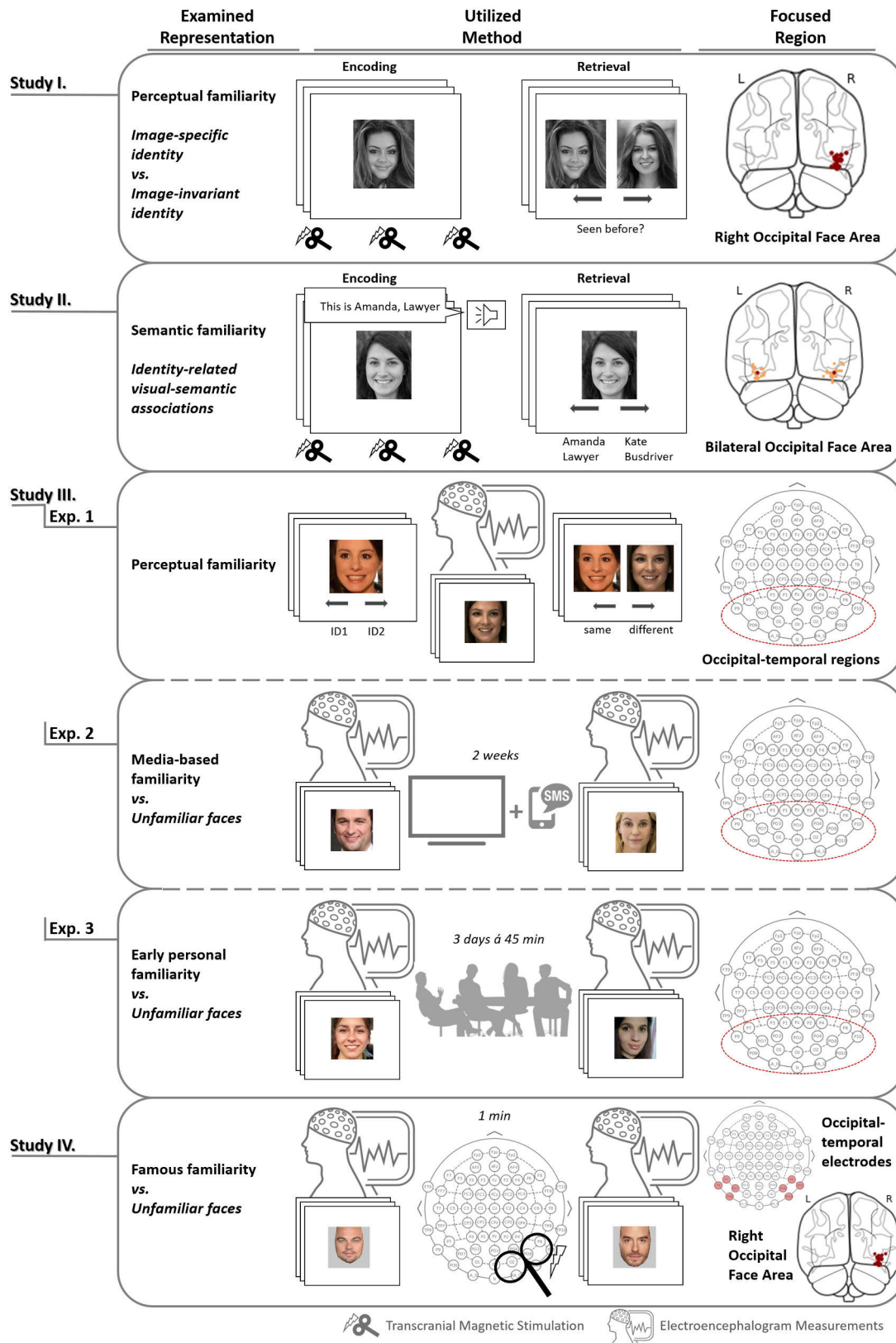


Figure 29: Overview of the studies presented in this Thesis: Study I, Study II, Study III including Experiment 1, 2 and 3 and Study IV. Depicted are the examined familiarity and/or identity representations, the utilized methods and paradigms to realize the purpose and the region we focused on.

The studies described in this Thesis collectively show that becoming familiar with a face gradually changes the (electrophysiological) representations of it in the occipital-temporal cortex. In the acquisition of a new identity via perceptual exposure or semantic information, the OFA plays a specific role. Connecting this early region of the face network with representations of familiarity, suggest a reconsideration of the hierarchical face-perception models with favour to distributed and recurrent models.

5.1 Face Familiarity

The familiarity of faces can be sorted into four approximate categories (Natu and O'Toole, 2011; Kovács, 2020). However, even if it seems intuitive, developing familiarity towards a face or getting to know a face is not a serial process (Kovács, 2020). The described levels above do not necessarily need to develop gradually, as the real-life process of familiarization is very versatile and dependent on multiple modalities (seeing images, videos, a real live person, hearing or reading about someone, etc).

In the following section representations of personally familiar and famous faces as well as face familiarity via visual exposure will be discussed as a part of Studies III and IV. The formation of personal-, media- and perception-based familiarization and their electrophysiological correlates are evaluated. Moreover, the differential processing of famous and unfamiliar faces is associated with the causal involvement of the OFA. Please note, that also Study I and II involve familiarity processing, although their focus lies on identity representations.

5.1.1 Representations of Established Familiarity in the N250 Time Range

Representations of established familiarity are visible in time range of the the N250 component in Study IV. Famous faces elicit significantly different amplitudes bilaterally in occipital-temporal electrodes than unfamiliar faces of the same gender, age and cultural background. This effect reliably pervades from 200 to 500 ms post-stimulus onset, corresponding to the results of Wiese et al. (2019) for personally familiar faces. We could not find influence of familiarity on the N170 component, which is rather related to general face detection (Eimer, 2000; Gosling and Eimer, 2011; Bentin and Deouell, 2000; Wiese and Schweinberger, 2008). Hence, we measured post-perceptual effects, which are based on the familiarity or identity of the presented faces. Even though tendencies of the familiarity effect are visible in the time range of

the late occipitotemporal negativity (LN, 400 - 800 ms; see Figure 27, p. 119), it did not reach significance, as it did for personally familiar faces (Wiese et al., 2019). Hence, the time range from 200 to 400 ms and the associated N250 is a reliable indication for familiarity representations over the occipital-temporal cortex. Later time points could correspond to higher face processing over medial or frontal regions.

This timing fits with the behavioural response of categorizing a face as familiar or unfamiliar, which is reported to be 310 ms and 370 ms respectively (Ramon et al., 2011). That response fits the N250 component with the minimal latency being due to the motor response (button press) following the decision.

After stimulating the OFA prior to the measurement, the familiarity effect was still ongoing. However, also an interaction effect between the face familiarity and the stimulation site (OFA vs. control) is visible in various occipital-temporal electrodes (see Table 1, p. 119). Interestingly, the effect originates from the response to familiar faces, as cTBS over the rOFA enhanced their amplitudes. This facilitatory effect hints towards inhibitory connections of the rOFA on other cortical sites. Stimulation with cTBS reduced activation in the rOFA which accordingly suppressed inhibition from this region. Hence, these disinhibited connections to regions of higher face processing, such as the ATL, which is involved in familiarity and semantic processing, then lead to the facilitation of familiarity representations (Chiou and Lambon Ralph, 2018; Rice et al., 2018; Tsukiura et al., 2010).

Further, these results show that the rOFA is involved in higher face processing, such as the familiarity status, to the point that its stimulation alters electrophysiological representations. This is supported by fMRI studies reporting activation in the OFA for famous or familiarized faces (Davies-Thompson et al., 2009; Amado et al., 2018; Hahn and O'Toole, 2017).

Event-related potentials were a helpful tool in exploring electrophysiological components of face familiarity since they provide solid comparability between several conditions. The focus of Study IV was to ascertain familiarity effects and if they are influenced by stimulating the rOFA and a first evaluation of the combination of EEG and TMS. In addition, this prevalent method offers many comparable studies to substantiate our interpretations. The next paragraph discusses the results of Study III, in which the analysis technique MVPA was utilized. Even though the direct comparison is aggravated due to the different approaches, these two methods were chosen because of their individual advantages. Compared to Study IV, in Study

III, we concentrated on the temporal dynamics of the formation of familiarity and identity representations and to detect more delicate effects.

5.1.2 Representations of Emerging Familiarity around 400 ms Post-stimulus Onset

Representations of emerging familiarity could be shown around 400 ms in Study III. Two familiarization strategies lead to this outcome: the familiarization via media exposure by watching a series and getting to know two identities personally for three days.

The media exposure was reached by letting the participants watch one season of a series involving the two identities to be familiarized (screen time: 2 hours and ~20 min) and additionally offering semantic information about them. Together, this approach encodes sufficient traces to decode via MVPA. The traces of familiarity were significant in the left occipital temporal regions only, which is rather connected to low-level feature processing Meng et al. (2012).

The personal familiarization was realized by three meetings for 45 minutes between the participants and two identities working in our group. These personal meetings left a lasting impression of the two learned faces. The familiarity decoding could be shown from 400 until ~1000 ms in both posterior hemispheres. Even though the additional information about the identities was not as controlled as in the media-based approach, seeing persons in real life formed a robust familiarity with them. Apparently the variability of perceptual input, like being exposed to their faces in various lighting conditions, viewpoints and face expression facilitates incidental encoding.

These two approaches seem rather comparable, as two individuals were observed speaking and interacting in natural settings for 2,5 hours. However, real-life interactions lead to a deeper impact of the related faces. A bidirectional relationship with mutual interaction apparently deepens the familiarity process. This might be due to non-visual sensory features (e.g. voice/perfume) and more importantly involuntary reactions on their faces to the participants, which is crucial for social coexistence.

Perceptual familiarization by repeatedly presenting various images of four identities, however, did not adequately encode faces to the point of decodable familiarization. This paradigm only offered pictorial cues, as images were presented visually and no other information was provided. It shows, that the feeling of familiarity towards a person is dependent on associated semantic information. Only when receiving further knowledge and connecting it to the face, one 'gets to know' someone properly and reliable identity representations can be built.

Comparing these correlates of familiarity around 400 ms post-stimulus onset with the N250 ERP familiarity effects in Study IV (from 200 - 400 ms), they emerge at a later time point. In Study III, representations of *emerging* familiarity were targeted. Hence, these correlates rather depict the process of 'getting to know' the face of a person and they are rather based on perceptual information which is connected to additional semantic knowledge stored in declarative recognition memory. Accordingly, this 'lateness' of the familiarity processing at 400 ms could be, among other reasons, due to feedback from the memory system. The effect in the N250 component, however is based on completely unfamiliar faces compared to faces, that are well known for years. Consequently, their representations are well trained and accessing them is a faster process (Ramon et al., 2011). For personally familiar faces compared to unfamiliar ones, the effect also starts in the N250 component and even remains until 800 ms post-stimulus onset (Wiese et al., 2019). When utilizing the MVPA approach, familiarity traces are detectable even earlier. Barragan-Jason et al. (2015) decoded single-trial ERPs and described effects from 140 to 160 ms and then from 250 ms with increasing accuracy in the later time ranges. Ehrenberg et al. (2020) showed with the analysis of dense MEG recordings a distinction of neural activity corresponding to familiar and unfamiliar faces from 100 to 350 ms in occipital temporal electrodes. However, a similar study only reports decodable familiarity traces in later time ranges (400 - 600 ms) (Dobs et al., 2018).

5.2 Face Identity

Compared to face familiarity, face identity is a perception with rather subtle representations. The feeling of having seen a person (familiarity) is easy to reach at various levels. However, it is hard to pin down the moment someone 'knows' the identity of a face. It is a matter of definition if face identity is either evident in the recognition of a face which has been seen before and the differentiation between two faces, or if it is a comprehensive understanding of the person related to the face. In this Thesis, we accordingly differentiate between the pictorial-based identity representations and the complex knowledge of a person, as well as both their unique neural representations.

Similar to face familiarity, face identity inherits various categories, depending on the quality and depths of the previous interaction. In the next section, Studies I, II and III will be discussed, which involve different forms of face identity. Semantically induced and perceptual based face

identity were studied concerning the involvement of the OFA. In addition, electrophysiological correlates of the latter, as well as face representations stimulated by media and personal interactions, were investigated.

5.2.1 Image-specific and -invariant Identity Representations

Identity representations in the OFA have previously been described as image-dependent (Davies-Thompson et al., 2009; Yovel and Kanwisher, 2004; Hoffman and Haxby, 2000). We developed Study I to test image-specific as well as -invariant identity representations in that area and evaluate the statement above. Examining both processes in one paradigm can assess previous studies and add another component to the conclusion. For that purpose, TMS was applied over the rOFA during the face encoding phase of a memory task. To reach image-*invariant* identity representations, the participants were trained on one identity with 30 different images. To test image-*specific* identity representations, 30 images of different identities were presented one single time. By applying a two-alternative forced-choice recognition task, recognition memory was tested in a subsequent retrieval phase.

First, the general recognition of the trained identity and to a lesser extent, for single presentation images laid above chance level, indicating the encoding of image-specific representations. This effect was independent of TMS stimulation, hence the delicate traces of images seen once are not interference-prone due to the altered OFA. However, only in the decision involving interference between image-invariant and image-specific representation, exactly these traces of image-specific identity were altered: the correct identification of old images (based on image-specific representations) was reduced after TMS over rOFA. This indicates that the OFA is involved in the encoding of image-specific face representations namely by differentiating them from other images. These results accordingly support previous studies, which allocate the OFA a role in image-specific face encoding and retrieval. Please note, that this outcome does not collide with studies, describing an involvement of the OFA in identity-specific (image-invariant) representations (Ambrus et al., 2017a). Only due to encoded image-invariant representations in the OFA, the image-specific traces could be altered due to their interference.

5.2.2 Non-visual Semantic Identity Representations

In Study II, the occipital face area was examined based on its involvement in identity related visual semantic associations. Encoding and accessing semantic information and memory is

part of higher processing steps, presumably located in the anterior temporal lobe and medial prefrontal cortex (Chedid et al., 2016; Cloutier et al., 2011). Experimentally, this was reached by showing a previously unfamiliar face and associating this person with semantic information. Here, their name and job were simultaneously presented acoustically, to not interfere with the visual perception. As half of the participants were stimulated over the right OFA and the other half over the left one (additionally to a control side), we could evaluate, whether the bilateral OFA is involved in this process.

The outcome showed, that the recall performance of the face-associated job titles was reduced after stimulation of the OFA during encoding. The face could not be reliably linked to the job title when the OFA was preoccupied due to the stimulation. This suggests a causal role of the OFA in the association of familiar faces with related semantic information. For this function, no hemispherical dominance can be reported. The associated job titles were better recalled than the names, probably as names are harder to remember than jobs (Burton et al., 2019). Tsukiura et al. (2010), utilizing a similar paradigm, also reported greater BOLD signals in the ATL for job title than for name retrievals. They described serial access of personal information of a face, starting with the activation of face-related information and then assessing person- and finally name-related semantic information (Bruce and Young, 1986). As this model is structured serially, strong feedback connections need to be incorporated, because the outcome of our study shows a semantic representation in an early face processing region, the OFA. Hence, the visual representation of the face and person-related semantic information such as the job are linked more closely in the complex organization of the face-network. It shows the necessity of re-evaluating the previous view, which stated that the sub-networks, corresponding to the recognition of a face and the retrieval of semantic knowledge, are considered relatively independent processes (Zhen et al., 2013).

The outcome of this study attributes the OFA an involvement in non-visual semantic associations to a face. This supports the outcome of a recent cross-domain priming study, which places associations between a face and the name in the OFA (Ambrus et al., 2019a). The OFA further plays a role in image-specific face representations, described in Study I, the learning of novel faces as well as identity-specific processing (Ambrus et al., 2017b,a). These results show that the OFA captures versatile functions in the face network and is not limited to low-level processing.

5.2.3 Representations of Emerging Identity 150 ms Post-stimulus Onset

Neural responses to unfamiliar and familiarized faces were collected in Study III. The familiarization process was realized in three categories based on different modalities (perceptual, media-based and personally). An overview of decodable identity representations in posterior occipito-temporal electrodes clusters is depicted in Table 2 for each experiment.

Table 2: Time ranges, in which identity representations were decodable after perceptual (Exp. 1), media-based (Exp. 2) and personally familiarization (Exp. 3) in Study III. Here, only correlates from the post-familiarization measurements in left and right occipital-temporal electrodes in the first 800 ms are depicted.

	perceptual		media-based		personally	
	left	right	left	right	left	right
fam	320 - 610	60 - 110	110 - 200	150 - 590	200 - 270	170 - 290
		260 - 330	220 - 320	620 - 700	360 - 440	330 - 440
		410 - 460	400 - 480	800 - 860		
			700 - 770			
unfam	130 - 260	110 - 170	110 - 170	110 - 180	650 - 740	/
	390 - 490	450 - 500	250 - 490	260 - 540	770 - 880	
	530 - 600	530 - 600	520 - 750	600 - 700		

The identity decoding is visible around 150 ms post-stimulus onset in both hemispheres for familiarized as well as for unfamiliar faces (see Figure 14, p. 80). This early-onset and the similar patterns between familiar and unfamiliar faces rather hint towards early visual differences between the identities as a basis for the decoding. A similar study utilizing media-based familiarisation also decoded identity representations after 90 - 250 ms post-stimulus onset (Dziura and Thompson, 2020). A MEG study, involving representations of the whole cortex, could decode identity selectively from 100 to 600 ms but only for familiar faces, probably due to the high familiarity of the famous faces (Dobs et al., 2018). Famous face identity was also decodable in an EEG study from 150 to 1100 ms in the right occipital-temporal cluster. After rejecting correlations based on low-level features by controlling for pixel dissimilarity, identity was decodable from 450 ms onwards (Ambrus et al., 2019b). By eliminating the pictorial basis for decoding, these correlations rather depict in depths representations of identity, involving complex person knowledge and memory recollection.

When comparing the temporal development of familiarity and identity representations, there are no interactions to report. They emerge independently from each other, hence being familiar with a face does not enhance the quality of identity representations in the course of this study. This is in line with familiarity and recollection of the involved memory performance (see *Face Identity* 1.3) (Yonelinas, 2001, 2002), which is based on differential processes and involve diverse brain regions (Brown and Aggleton, 2001). As we did find correlates of face familiarity but no evident identity-specific representations based on memory recollection, a dissociation between familiarity and recollection can be indicated.

5.3 The Versatile Role of the Occipital Face Area in Face Processing

In the course of this Thesis, three learning paradigms were introduced, regarding various levels of face identity and familiarity (Study I, II & III), Study IV utilized already familiar identities.

The outcome of Studies I, II, IV, in which the causal role of the OFA was examined, shows its versatile involvement in the face network. The functions of the occipital temporal cortex, including the OFA, comprise perceptual face processing, identity representations and the association to further semantic information. The latter suggests a close connection between the OFA and the ATL, which encodes semantic face information (Chiou and Lambon Ralph, 2018; Rice et al., 2018; Tsukiura et al., 2010). This functional interaction is based on robust structural connectivity between ATL and OFA (Pyles et al., 2013). Correspondingly, semantic aspects of object recognition show functional top-down connections from the ATL to the ventral temporal cortex (Chiou and Lambon Ralph, 2016). Hence, the sole role as an entry point to the face network does not do justice to the OFA. The interaction of the OFA with regions involved in higher face processing prompts a re-evaluation of the feed-forward serial face network. This necessity further becomes apparent in the duality of the identification process, with bottom-up (sensory) and top-down connections (associative, predictive, mnemonic) (Kovács, 2020). Face recognition involves parallel bottom-up and top-down interactions between core and extended network nodes. Barbeau et al. (2008) report neurophysiological evidence consistent with both, feed-forward as well as feedback neural signalling. An adaptation is necessary to support models that include distributed and recurrent interactions. Solomon-Harris et al. (2013) suggests a non-hierarchical, global-to-local model with re-entrant connections between the OFA and other face processing areas. They attribute a more complex role to the OFA, as well.

Additionally to the top-down network exchange, inter-hemispherical connections are crucial as well. Alongside the causal role of the rOFA in the processing of familiar and the encoding of unfamiliar faces, the bilateral effects in Study II and IV show a close connection between the two occipital-temporal hemispheres. Inter-hemispheric integration of visual information is reported after visual input to only one hemisphere (Kietzmann et al., 2015). It depicts a strong cooperation between the two occipital-temporal hemispheres, which makes compensating structural changes possible, for example after trauma.

Theoretical models of neural networks support the need for a more complex approach with bi-directional exchange between the involved regions. It has been shown, that recurrent deep neural network models outperform parameter-matched feed-forward models for object processing (Kietzmann et al., 2019). Further virtual cooling experiments, in which regions of the model have been excluded, depict the importance of lateral and top-down connections. Another conclusion of a computational model is, that becoming familiar with a face relies on both bottom-up statistical image descriptions as well as top-down processes that convey the hallmark of the face (Kramer et al., 2018).

5.3.1 Reciprocal Interaction between the Occipital Face Area and Higher Face Regions

That the OFA plays a role in higher face processing has been discussed multiple times in the course of this Thesis. What is yet to be addressed is how its involvement in higher face processing functions is achieved. Most likely it is due to interplay with regions of the extended face network, such as the ATL. Feed-forward and feedback connections between these two regions have been reported (Chiou and Lambon Ralph, 2016; Pyles et al., 2013). However, the influence of transcranial magnetic stimulation of the OFA on this connection is yet to be determined. Handwerker et al. (2020) describes reduced resting-state connectivity across the extended face processing network after TBS over the rpSTS. Our results from the studies including the stimulation of the OFA are not coherent, as they report inhibitory (Study I & II) as well as excitatory effects on face processing (Study IV). One explanation can be given by a developed model regarding the interaction of the OFA and ATL (see Figure 30).

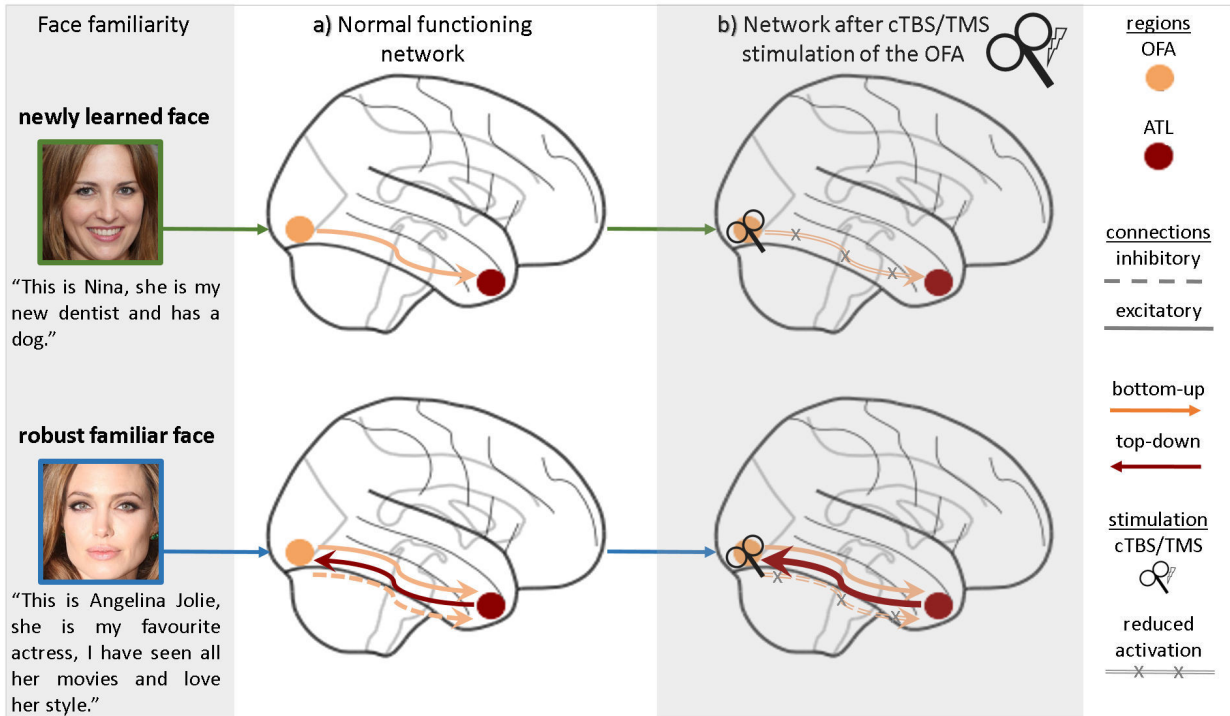


Figure 30: This model describes the twofold connections from the OFA to the ATL, depending on top-down modulatory signals. Column **a**) depicts the network without interference: After seeing a newly learned face (green input-up), excitatory connections (yellow arrow) from the OFA to the ATL connect the pictorial input with semantic information. After seeing a familiar face (blue input- below), the stored knowledge about the person reaches the OFA via top-down signals from the ATL (red arrow), who responds with inhibitory feedback (dotted yellow arrow). This way, the stored knowledge does not interfere with possible new faces, which could be learned. Column **b**) shows the impact of cTBS or TMS of the OFA on this network. The excitatory connection between the OFA and ATL, associating a new face to additional information is reduced (up). Hence behavioural performance in related tasks is declined (Study II). When processing a known face, stored semantic information gets recalled but the inhibitory response from the OFA to the ATL is now reduced. As a result, the familiarity response is not inhibited (thick red arrow) which leads to a positive modulation of electrophysiological signals to familiar faces (Study IV).

I propose, that the input from the OFA to the ATL can be both excitatory as well as inhibitory. The state of the activation depends on whether the OFA receives feedback from the ATL or not. If top-down signals are coming from the ATL to the OFA, the response back (from the OFA to the ATL) is inhibitory. That is the case, when seeing a familiar face (Fig. 30, a) blue input). An existing representation of the face and connected semantic knowledge are already present, so the ATL is active. This information gets signalled top-down to be processed in early regions, like the OFA (see Study II), which in return inhibits the ATL. That is visible in the enhanced N250 familiarity components after reducing the OFAs activation via TMS. The results show, that the inhibitory response from the OFA to the ATL was reduced (see Study IV; Fig. 30,

b; blue input). On the other hand, if no signal is reaching the OFA from the ATL, the input from OFA to ATL is excitatory. That is the case when getting to know a new face. No established representations and information are stored and the input from the OFA to the ATL is excitatory (Fig. 30, a; green input). This way, face images are connected with information about the person and a representation if this face gets established. That is visible in the outcome of Study II, in which the learning process and the excitatory connection were reduced after TMS of the OFA (Fig. 30, b; green input). As a consequence, the recall of job titles associated with the face decreased.

Why the initial excitatory input from the OFA to the ATL after seeing a familiar face is not influenced by stimulation, could be due to the following reasons: First, this connection is already established and not in the fragile state of being build. Second, it is only a query for the retrieval of semantic information as opposed to the modulatory inhibitory response, which probably is a more intense and prolonged activity.

This model also applies to a recent behavioural study involving famous faces and stimulation over the rOFA (Ambrus et al., 2017a). In the condition involving the same identity (sameIMG, sameID) no stimulation effect is visible. As there is no interference between multiple identities, eventually reduced inhibition from the OFA to the ATL does not lead to behavioural effects. Only in the 'diffID' condition, in which the participants get primed with a face from another identity, top-down information from the ATL are crucial. After stimulation of the OFA, the performance is enhanced, as the input regarding the identity from the ATL receives less inhibition from the OFA. The same outcome, better performance in the incongruent condition, is reported when priming with names instead of faces (Ambrus et al., 2019a). Accordingly, the model proposing excitatory as well as inhibitory connections from the OFA to the ATL is not limited to pictorial input but is expandable to cross-domain interactions as well.

The differential processing of familiar and less familiar faces is apparent in this model. The proposed reciprocal interactions between the OFA and ATL present an explanation in regards to the underlying anatomical causes. Further, it is apparent that the OFA is involved in the processing of both, familiar and unfamiliar faces.

This model about the top-down modulatory signals from ATL and the resulting input-dependent signals from the OFA to the ATL is in line with a reported feed-forward connection between occipital and temporal areas within the face and body networks in the human visual cortex (Sadeh et al., 2011). It further refines one aspect of the bottom-up/ top-down duality of

the identification process (Kovács, 2020; Kramer et al., 2018).

Top-down monitoring and executive control on face recognition processing in the temporal lobe is also reported for other regions of the extended network, such as the ventrolateral prefrontal cortex (PFC) (Rapcsak, 2019). If this model only concerns the connections between the OFA and the ATL or higher face processing regions in general, can not be answered in the course of this Thesis. This conclusion should be considered with caution, as the present studies only offer a comparison between the results of behavioural changes with electrophysiological responses. Multiple further studies would be needed to examine the feedback connections from the OFA to higher face regions to properly evaluate this proposal.

In conclusion, bottom-up connections of the OFA are inhibitory in response to top-down signals from the ATL otherwise, they are excitatory. One possible reason for this input-dependent signal from the OFA to the ATL could be to 'clear the way' for the purpose to learn new faces. Sending inhibiting feedback after getting input about already established representations leads to less interference between an existing and a to be build idea of a face. That makes this learning process less error-prone. These developments suggest a key role to the OFA in getting to know a face (Study II), individual face recognition (Study IV) as well as differentiating between two identities (Study I). This is supported by Solomon-Harris et al. (2013), who report involvement of the OFA in face recognition and the FFA in face detection (but see Tsantani et al. (2020) for a different conclusion).

5.3.2 The Occipital Temporal Cortex in Recognition Memory

In Study III, we report correlates of face familiarity but can not decode identity-specific representations, which are based on memory recollection. This dissociation allows conclusions to be drawn about the involved anatomical areas. The formation of familiarity based on media and personal exposition involves the anterior temporal and perirhinal cortex. Structures that are active during recollection such as the hippocampus as well as prefrontal and parietal areas are not involved (Brown and Aggleton, 2001). However, activation in the hippocampus is reported after seeing famous (Ishai et al., 2002; Rey et al., 2020) and personally familiar faces (Ramon et al., 2015). This suggests that the retrieval of semantic information in the ATL is ongoing in the learning process of these paradigms, but the involvement of the declarative/associative memory is not yet reached (Eichenbaum, 2000; Mayes et al., 2007; Olsen et al., 2012; Ranganath,

2010).

Further, the results of Study I have been evaluated in regards to recognition memory. They suggest that the rOFA is rather involved in recollection than familiarity. This embraces the previously reported connection of the OFA to higher face processing areas, as recollection is accompanied by active prefrontal and parietal areas and hippocampus.

6 Outlook

The studies reported in this Thesis are part of a research strand, which aims to re-evaluate the functional structure of the core network of face processing. The focus of this Thesis is on the occipital face area (OFA), which is proven to be involved in more versatile functions than previously reported.

6.1 Relevance

The outcome of the studies presented, shines a light on a more complex setup of the network, with multiple feed-forward as well as feedback connections between all involved high- and low-level regions. Furthermore, this also involves inter-hemispherical interaction and the possible delegation of functions of lesioned regions to neighboured areas after trauma.

This knowledge should be considered in future face recognition models. Not only functionally and structurally motivated networks should be evaluated but also computational models, which until now use strictly feed-forward architecture neural networks (Blauch et al., 2020; Kramer et al., 2018) will need to work in more complex convoluted interactions, which are an inherent part of the face network.

Additionally, based on this adapted face network, algorithms of programs using machine learning for face recognition in photos and videos could profit from including neurally based networks into their calculations. Basing technology on principles extracted from well-working systems of nature is an often-used source for further development of technologies.

6.2 Open Questions and Limitations

As a general methodological constraint of the TMS approach, a possible propagation of the stimulation effect from the target area towards other processing stages of the network needs to be named (Ruff et al., 2009; Siebner et al., 2009). After stimulating the right hemisphere in Study IV, a bilateral effect was visible. The connection between the two hemispheres is so elaborated, that the stimulation affected both sides equally. However, this propagation could limit the causal interpretation of any TMS study, as there is no control over which neighboured or connected regions are affected as well. Further, possible inhibitory or excitatory connections of the stimulated region could also affect behavioural or electrophysiological changes, which

takes the causal interpretation of the ‘virtual lesion’ effect to a more complex level.

One limitation arose from the side effects of transcranial magnetic stimulation. Originally, Study II was planned to be repeated with the stimulation of the area ATL, which is part of the extended face network. As this region is reported to be involved in connecting faces with corresponding semantic information, it would have been interesting to evaluate, whether its stimulation would also affect the visual semantic associations. However, as the ATL is located at the anterior pole of the temporal lobe, many muscles from the face and the neck are located over this area (approximately above the ear). Hence, when stimulating the ATL, all the superjacent muscles get stimulated and activated as well. This leads to face and neck ticks, which make a visually based paradigm hard to realize. Further, it can be an unpleasant experience, depending on the sensitivity of the participant. Accordingly, after trying this stimulation type in a pilot experiment, we concluded to not realize this study. Additionally, the applied localizer in the fMRI measurements did not result in reliable coordinates of the ATL in every participant. That is due to the proximity of this region to the ear canal, which leads to noisy data. A great number of these open questions can be answered with follow-up studies, which will be discussed in the next paragraph.

6.3 Future directions

After having discussed the presented studies in detail, the next paragraph will point out possible follow-up examinations and fruitful reanalysis steps of the available data.

To revisit the discussed limitation regarding TMS experiments including the ATL, multiple steps could be applied to realize them. First, to reach a reliable acquisition of coordinates of the ATL, a careful alignment of the field of view is necessary. The occipital as well as the anterior part of the cortex needs to lie within the area, which requires an experienced hand. Second, the stimulation protocol has to be adapted to the needs of this purpose. One measure would be to adapt the paradigm from online TMS during the experiment (e.g. Study I and II) to be suited for offline cTBS stimulation prior to the experiment (e.g. setup of Study IV). This way, the activation of the facial muscles would be ongoing before the experiment and not distract from the paradigm. Further, this would lead to a reduced stimulation intensity (approximately from 65 % to 40 - 45 % maximal stimulation output) and a more tolerable experience. A strong recommendation would also be, to measure each participants’ individual resting motor thresh-

old (RMT, the minimal intensity to which a muscle response occurs to stimulation) and then stimulate at 80 % of this intensity (Chiou and Lambon Ralph, 2018). This would adapt the physiological responses to an individual tolerable level of each participant.

The two different analysis approaches in the studies involving EEG measurements have been discussed previously in 5.1.1. Now, that the combined EEG and TMS approach has been proven useful, further analysis of the gained data is reasonable. Hence, the next coherent and interesting step would be to reanalyse the data of Study IV with the more sensitive methodological MVPA approach. That would allow a direct comparison between cortical correlates to familiar faces with (described in this study) and without (Ambrus et al., 2019b) the influence of cTBS over the OFA. The effects visible in the ERP components draw a clear picture of the causal role of the OFA in this process. However, the neural correlates evaluated by MVPA allow a more sensitive temporal evaluation. It would give further insights about identity as well as familiarity representations over the occipital-temporal lobe and how they are connected to the functions of the rOFA.

Moreover, it would be beneficial to replicate the three learning paradigms of Study III with the combined EEG-TMS methods approach from Study IV. After the familiarization period, half of the participants receive cTBS over the Vertex, the other half over rOFA prior to the post EEG measurement. That would let us not only assess electrophysiological familiarity and identity representations in the OFA for famous faces but also during the process of getting to know someone personally, media-based or via visual exposure. The knowledge from Study IV would also influence the electrode clusters, whose response pattern is the basis of the created RDMS. Instead of an integrated approach with six different electrode clusters over the right and left posterior, central, and anterior cortex, a focus on the occipito-temporal regions would be beneficial.

6.4 Conclusion

Summarizing the four studies discussed in this Thesis leads to the following conclusion: The rOFA is participating in the formation of image-specific face representations. The OFA is further involved in the process of getting familiarized with previous unknown faces via semantic information. We can elicit familiarity representations at around 400 ms with a media-based and personal familiarization process but not after perceptual based familiarity. Identity repre-

sentations are at this level of face learning all based on pictorial information. The differential processing of familiar and unfamiliar faces is visible in the N250 ERP components, which are modulated by the rOFA.

To evaluate the proposed model (Fig. 30, 148), additional studies are necessary. A face-learning paradigm including cTBS of the OFA and EEG measurements would be the next logical step. The outcome could answer if electrophysiological responses of newly familiarized faces are reduced after TMS of the OFA, as the described model proposes. The first experiments should focus on the right hemisphere because it is reported to be dominant in the top-down control of visual attention and perception (Karnath et al., 2002).

This Thesis shows, that connecting the investigation of causal functions of network-related regions with electrophysiological responses is a rewarding approach. In the future, the paradigms used in the setup should also include behavioural tasks, to examine the process comprehensively. These could be the next steps to understand the complexity of face processing in the occipital temporal cortex. This research strand is under constant development. Pitcher and Ungerleider (2021), for instance, recently established evidence to suggest a third visual pathway, specialized for social perception, to complement the ventral 'what' and dorsal 'where' pathway. Experiments that focus on a single region of a complex network, such as those described in this work concerning the OFA, provide valuable foundations. These enable conclusions about connections between involved regions, the evaluation of functional systems as well as adapting models of face recognition.

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Index of abbreviations

TMS Transcranial Magnetic Stimulation

cTBS Continuous Theta-burst Stimulation

tDCS Transcranial Direct Current Stimulation

EEG Electroencephalogram

fMRI Functional Magnetic Resonance Imaging

MEG Magnetoencephalogram

BOLD Blood Oxygen Level Dependence

(r)OFA (right) Occipital Face Area

FFA Fusiform Face Area

(p)STS (posterior) Superior Temporal Sulcus

IPL Inferior Parietal Lobule

IFG Inferior Frontal Gyrus

IOG Inferior Occipital Gyri

ATL Anterior Temporal Lobe

aFP Anterior Face Patch

PC/PCC Precuneus/ Posterior Cingulate Cortex

MTL Medial Temporal Lobe

AMY Amygdala

MPFC Medial Prefrontal Cortex

ID Identity

ANOVA Analysis of variance

ERP Event-Related Potential

LN Late Occipitotemporal Negativity

MVPA Multivariate Pattern Analysis

RSA Representational Similarity Analysis

LCA Linear Classification Analysis

mean, M Arithmetic mean

sem Standard error of mean

SD Standard deviation of mean

min minute

(m)s (milli)seconds

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Statutory Declaration

I, Charlotta Eick, declare that the dissertation 'The Role of Occipital Temporal Cortex in the Formation of Face Familiarity and Identity' is a result of my personal work and that no other than the indicated sources have been used for its completion. Furthermore, I assure that all quotations and statements that have been inferred literally or in a general manner from published or unpublished writings are marked as such.

This work has not been used, neither completely nor in parts, for academic grading or to pass any previous examination or has been handed in as a dissertation in another university.

I am aware of the current doctoral regulations (Promotionsordnung) of the Faculty of Social and Behavioural Sciences. The assistance of a commercial doctoral agency (Promotionsvermittlung) has not been utilized and no paid services related to the content of the submitted thesis have been used.

Date: _____ Signature: _____

Contributions of Authors

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Study I. I have seen you once before - evaluation of image-specific and -invariant identity representations in the occipital face area

The research question as well as the idea and design of how to evaluate it was developed by Prof. Dr. Gyula Kovács and Dr. Géza Ambrus. The experimental program was realized by Dr. Ambrus. He and Master student Antonia Eisele acquired and prepared the stimuli as well as collected the data. The data was analysed by Dr. Ambrus, Antonia Eisele and me and interpreted by Prof. Kovács, Dr. Ambrus and me with helpful input to the topic of recognition memory by Dr. Agnes Szöllősi and Prof. Dr. Mihály Racsmány. On that basis, I researched suitable literature and wrote the manuscript, for that Dr. Szöllősi contributed two paragraphs about the outcome in the context of recognition memory. Final discussion and revision of the manuscript included all stated authors Prof. Kovács, Dr. Ambrus, Dr. Szöllősi, Prof. Racsmány and me.

Study II. The occipital face area is causally involved in identity-related visual-semantic associations

The idea for this study came from Prof. Kovács and Dr. Ambrus in the course of the research strand 'The ventral visual pathway and the construction of identity-specific representation'. Again Dr. Ambrus designed and programmed the used paradigm, as well as prepared the used stimuli together with Bachelor student Lisa Röhrig. The data for the right hemisphere stimulation group was collected by Dr. Ambrus and Lisa Röhrig and me, the left side stimulation group was measured by Bachelor student Moritz Stabe and me. I analysed the data and interpreted the outcome together with Prof. Kovács. I researched the literature and wrote the manuscript, which was discussed and revised by Prof. Kovács, Dr. Ambrus and me.

Study III. Getting to know you: emerging neural representations during face familiarization

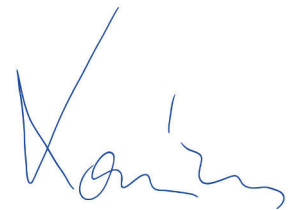
The evaluation of electrophysiological correlates for different familiarity levels was initiated by Prof. Kovács and Dr. Ambrus. The design of the experiments was developed by Prof. Kovács and Dr. Ambrus, who also created the used paradigms. To realize this purpose, Dr. Ambrus and I collected and prepared the suitable stimuli as well as realized the experimental setup.

The data was then collected by Dr. Ambrus and me. The design of the data analysis was developed by Prof. Kovács, Daniel Kaiser and Dr. Ambrus, who then analysed the data. The interpretation and course of the manuscript were thought of by Prof. Kovács and revised by Dr. Ambrus, Daniel Kaiser and me. Also, the main literature research and manuscript writing was done by Prof. Kovács with support from Dr. Ambrus and me, especially in the creation of the figures and supplementary material.

Study IV. Inhibition of the occipital face area modulates the electrophysiological signals of face familiarity positively: a combined cTBS-EEG study

The aim to combine EEG and TMS to research face processing originated from a meeting between Prof. Kovács and Prof. Dr. Rossion. This research idea was then elaborated by Prof. Kovács and me and I acquired the stimuli and created the experiment (based on a paradigm by Dr. Ambrus) as well as the experimental setup. I collected the data and analysed it with the support of Prof. Kovács. We interpreted the outcome and created the manuscript together, with the introduction and discussion being written by him and the methods and results sections being written by me. The paper was finalized by Prof. Kovács, Dr. Ambrus and me.

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Charlotta Eick

Prof. Gyula Kovács

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Cheers,

Charlotta Eick

List of Scientific Publications

Paper

Eick, C. M., Ambrus, G. G., Kovács, G., (2020) Inhibition of the occipital face area modulates the electrophysiological signals of face familiarity positively: a combined cTBS-EEG study. *Cortex* [under review]

Eick, C. M., Kovács, G., Eisele, A., Szöllősi, A., Racsmány, M., Ambrus, G. G. (2020) I have seen you once before- evaluation of image-specific and -invariant identity representations in the occipital face area. *Neuropsychologia* [under review]

Ambrus, G. G., **Eick, C. M.,** Kaiser, D., Kovács, G. (2020) Getting to know you: emerging neural representations during face familiarization. *The Journal of Neuroscience* [second review]

Eick, C. M., Kovács, G., Rostalski, S. M., Röhrig, L., Ambrus, G. G. (2020). The occipital face area is causally involved in identity-related visual-semantic associations. *Brain Structure & Function* 225, pp. 1483–1493. DOI: 10.1007/s00429-020-02068-9

Eick, C. M., Ahmadi, K., Sweeney-Reed, C. M., Hoffmann, M. B. (2019). Interocular transfer of visual memory - Influence of visual impairment and abnormalities of the optic chiasm. *Neuropsychologia* 129, pp. 171–178. DOI: 10.1016/j.neuropsychologia.2019.03.018.

Conferences

[Poster] **Eick, C. M.,** Ambrus, G. G., Kovács, G. (2020) Getting to know you: altered response in occipital-temporal cortex after personal familiarization *Face: Familiarity, 20st* (Virtual) Annual Meeting of the Vision Sciences Society (V-VSS)

[Talk] **Eick, C. M.,** Yan, X., Rossion, B., Kovács, G. (2020) Automatic detection of familiarity in face selective cortical areas: A cross-cultural study *Symposium: Advances in person perception research: Processing identity and emotion in faces and voices, 62nd* Tagung experimentell arbeitender PsychologInnen (TeaP)

[Poster] **Eick, C. M.,** Ambrus, G., Röhrig, L., Rostalski, S. M., Amado, C., Kovács, G. (2018) Encoding of person identity information in the occipital temporal area: A TMS study. *Faces, 41st* European Conference on Visual Perception (ECVP)