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Neural correlates of non-familiar face processing

PhD thesis booklet

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Contents

Abbreviations	2
1 Introduction	3
2 Methodology	4
3 Research questions	5
4 Thesis I.	5
5 Thesis II.	6
6 Thesis III.	7
7 Thesis IV.	8
8 Discussion	9
List of publications related to thesis	14
References	14

Abbreviations

BOLD	blood oxygenation level dependent
DCM	Dynamic Causal Modelling
EEG	electroencephalography
ERP	event-related potential
FAE	face after-effect
FFA	fusiform face area
fMRI	functional magnetic resonance imaging
LO	ventral-anterior LOC
LOC	lateral occipital complex
MFS	multiple face settings
OFA	occipital face area
RF	receptive field
ROI	region of interest
V1	primary visual cortex

1 Introduction

This work will approach the neuronal background of non-familiar face perception with behavioural, electrophysiological and functional imaging techniques. Face processing is one of the most widely researched topics of cognitive science due to the importance of faces in social life. In the present work we aimed to examine face perception among ecologically valid circumstances. Even though many experiments have dealt with faces, most of them had low ecological validity. In everyday life we rarely see faces in isolation and under perfect visual conditions. To model these effects participants made two-alternative forced-choice decisions based on faces. We applied three methods to make face-relevant decisions more complex and more valid ecologically: first we added noise to the stimuli, second we morphed¹ the target stimuli and third we presented the target faces concomitantly with other faces.

In the first study we added Fourier phase-noise or overlapping meaningful images to the stimuli, in the second study the gender information of faces were modified with morphing, while in the third study target faces were presented among other faces. In the fourth study the underlying neuronal mechanisms of face and object processing was modelled using effective connectivity analyses. The applied stimuli in all studies were based on the face database of our laboratory (see Kovács et al. (2005)), consisting of non-familiar (everyday models, unknown by the subjects) faces. With constructing an ecologically valid set of stimuli and paradigms we may be able to explore the neural correlates of face perception among everyday conditions and our results may be generalizable for the entire population.

¹In morphing we transform smoothly one stimulus to another one, in a way that given points of the input stimulus are moved step-by-step into given points of the output stimulus.

2 Methodology

In the present dissertation four set of experiments are included. All the participant were university students from the Budapest University of Technology and Economics and from the University of Regensburg. All subjects had normal or corrected-to-normal vision and provided their written informed consent. The ethics committee of the Budapest University of Technology and Economics and of the University of Regensburg approved all experiments. Altogether 93 university students participated in the experiments (48 females) with an average age of 25.8 yrs (sd = 6.1 yrs).

We measured behaviour, electrophysiological and imaging correlates of face perception. In the event-related potential (ERP) experiment continuous EEG was recorded via 64 Ag/AgCl scalp electrodes (BrainAmp, Brain Products GmbH), mounted in a plastic cap. The experiment was carried out in an electrically and sound attenuated room. EEG data was analysed offline by Brain Vision Analyzer (1.05.0002; Brain Products GmbH). Grand averages were calculated for each channel, subject and condition separately. The usual face-evoked ERPs for our stimuli, composed of a positive peak at around 100ms (the P100), followed by a large negative peak (the N170) and a second positive peak at around 220 ms after stimulus onset (P220). Occipito-temporal channels (P7, P8, PO7, PO8) were analyzed bilaterally for assigning the latency and amplitude values of these ERP components.

In the fMRI experiments imaging was performed using a 3-Tesla MR Head scanner (Siemens Allegra, Erlangen, Germany). For the functional series we continuously acquired images and high-resolution structural images were acquired using a magnetization EPI sequence. Image processing was carried out with SPM5 and SPM8 (Wellcome Department of Imaging Neuroscience, London, UK) under Matlab. Region of interest (ROI) analyses were based on the results of separate functional localiser runs and were carried out with MARSBAR 0.42 toolbox for SPM (Brett et al. (2002)).

The location of face responsive areas was determined individually.

3 Research questions

In the present thesis neural correlates of non-familiar face processing were measured. For producing ecologically valid situations, faces were presented either with added noise or in the company of other faces.

The main questions were the following:

1. How does the nature of added noise influence face-relevant decisions? What are the electrophysiological correlates of the different types of added noise? (Nagy et al. (2009))
2. Does a face after-effect emerge in case of multiple face settings (MFS)? What are the neural correlates of the adaptation? (Nagy et al. (2012b))
3. Does parallel stimuli presentation trigger mutual interactions? What are the correlates of sensory competition among faces? (Nagy et al. (2011))
4. What brain areas participate in processing face and object stimuli and how is this network organized? (Nagy et al. (2012a))

4 Thesis I.

In case visual face processing the nature of added noise has an impact on the neural process of perception: Fourier-phase randomized noise reduces the face N170 component, while an overlapping meaningful stimuli only effects the processing later, around 200 - 250 ms after stimulus presentation.

The processing of any noisy stimuli requires extra effort from the nervous system. Several electrophysiological studies proved that the processing of noise starts approximately 150 - 200 milliseconds after stimulus onset. This is suggested by the fact that the amplitude of the face-selective N170 component has been reduced and its latency is prolonged by adding Gaussian noise to a face stimulus while the earlier P100 component is not influenced by added noise. While previous studies tested the electrophysiological correlates of noisy face perception in humans, the nature of added noise has not been studied yet in relation to face processing. Our goal was to distinguish the effects of added phase-noise from that of another irrelevant, overlapping non-face object (a car) on the electrophysiological correlates of human face processing. Subjects performed a two-alternative gender discrimination task with seven levels of difficulty, equalised between the phase-noise and overlapping object conditions. We found that the first component where an amplitude reduction took place was the N170 component when adding phase-noise to the face stimuli but not in the overlapping object condition. The amplitude of the later positive P220 component, on the other hand, increased significantly in both noisy conditions. Our results suggest that the processing of phase-noise starts in the time range, reflected by the N170 component, while the interaction of a face and of another overlapping irrelevant stimulus does not happen until the P220 component (Nagy et al. (2009)).

5 Thesis II.

Spatially non-overlapping multiple face settings are able to trigger face after-effect and this effect is localized in the fusiform face area (FFA), while the hierarchically subordinate occipital face area (OFA) is responsible for the position-specific components of adaptation.

Adaptation to a given face leads to face-related, specific after-effects. Recently,

this topic has attracted a lot of attention because it clearly shows that adaptation occurs even at the higher stages of visual cortical processing. However, during our every-day life, faces do not appear in isolation, rather they are usually surrounded by other stimuli. Here, we used psychophysical and fMRI methods to test whether humans adapt to the gender properties of a composite multiple face stimulus as well. As adaptors we used stimuli composed of eight different individual faces, positioned peripherally in a ring around a fixation mark. We found that the gender discrimination of a subsequent centrally presented target face is significantly biased as a result of long-term adaptation to either male or female multiple face settings (MFS). Similar to our previous results with single-face adaptors (Kovács et al. (2008)), a concurrent functional magnetic resonance imaging (fMRI) adaptation experiment revealed the strongest blood oxygenation level dependent (BOLD) adaptation bilaterally in the FFA. Our results suggest that humans extract the statistical features of the multiple face stimulus and this process occurs at the level of occipito-temporal face processing (Nagy et al. (2012b)).

6 Thesis III.

Concurrent presentation of faces trigger mutual interactions, the so called sensory competition. The activation reduction is dependent on the number and actual position of the presented face stimuli and localized in the fusiform face area (FFA) and in the lateral occipital complex (LOC).

The concurrent presentation of multiple stimuli in the visual field may trigger mutually suppressive interactions throughout the ventral visual stream. While several studies have been performed on sensory competition effects among non-face stimuli relatively little is known about the interactions in the human brain for multiple face stimuli. In this study we analyzed the neuronal basis of sensory competition in an

event-related fMRI study using multiple face stimuli. We varied the ratio of faces and phase-noise images within a composite display with a constant number of peripheral stimuli, thereby manipulating the competitive interactions between faces. For contralaterally presented stimuli we observed strong competition effects in the FFA bilaterally and in the right LOC, but not in the OFA, suggesting their different roles in sensory competition. When we increased the spatial distance among pairs of faces the magnitude of suppressive interactions was reduced in the FFA. Surprisingly, the magnitude of competition depended on the visual hemifield of the stimuli: ipsilateral stimulation reduced the competition effects somewhat in the right LOC while it increased them in the left LOC. This suggests a left hemifield dominance of sensory competition. Our results support the sensory competition theory in the processing of multiple faces and suggests that sensory competition occurs in several cortical areas in both cerebral hemispheres (Nagy et al. (2011)).

7 Thesis IV.

By performing effective connectivity analyses we found that ventral-anterior LOC (LO) is included in the core-network of face-processing. This area is linked to the FFA and OFA with bidirectional direct connections. Face and object inputs are not separated in this low level of face-processing.

The perception of faces involves a large network of cortical areas of the human brain. While several studies tested this network recently, its relationship to the ventral-anterior LOC (LO) cortex known to be involved in visual object perception remains largely unknown. We used fMRI and Dynamic Causal Modelling (DCM) to test the effective connectivity among the major areas of the face-processing core network and LO. Specifically, we tested how LO is connected to the FFA and OFA and which area provides the major face/object input to the network. We found

that LO is connected via significant bidirectional connections to both OFA and FFA, suggesting the existence of a triangular network. In addition, our results also suggest that face- and object-related stimulus inputs are not entirely segregated at these lower level stages of face-processing and enter the network via the LO. These results support the role of LO in face perception, at least at the level of face/non-face stimulus discrimination (Nagy et al. (2012a)).

8 Discussion

To summarize the main findings, in the *first study* (Nagy et al. (2009)) we showed that the nature of added noise alters the processing of faces. We found that added phase noise and overlapping images resulted in a similarly weak behavioural performance, but the neural background differs due to the nature of the noise. Phase noise is already processed at around 160 - 200 ms after stimulus presentation, therefore the amount of added noise is visible on the amplitude and latency of the N170. As we added overlapping meaningful stimuli to the faces, the processing of the interaction between the non-attended meaningful image and the face did not start before the P220 component. Thus, we can conclude that the N170 and P220 components of the face evoked ERP are affected differentially by Fourier randomization and overlapping irrelevant non-face objects.

In the *second study* (Nagy et al. (2012b)) we tested whether multiple face settings (MFS) evoked face after-effect (FAE) and measured the neural correlates of the adaptation. In a preliminary study we proved that participants were able to spread their attention across the MFSs and process the setting in a global manner. This fact encouraged us to examine the nature of after-effects triggered by MFSs. If faces are represented in a multidimensional face space (Webster and MacLin (1999), Leopold et al. (2001), Anderson and Wilson (2005)) and humans represent the statistical

properties of an MFS then adapting to them would shift the mean of the space systematically, leading to FAE on the behavioural level. The main findings are the following: (1) MFSs are able to trigger FAE, they bias the perceived gender of the target stimulus on the behavioural level, and (2) neural correlates of this effect are visible in the fusiform face area (FFA), where BOLD reduction was found, while such effects did not appear in the occipital face area (OFA).

The existence of this effect proves that the human brain is able to average information from distinct spatial locations and this average can bias perception. Similarly to other face adaptation experiments (e.g. Rhodes et al. (2003); Fox et al. (2009); Xu et al. (2009); Afraz and Cavanagh (2009); Cziraki et al. (2010)) we found signal reduction in face-relevant FFA. Besides this well-documented effect we did not find any adaptation effect in the OFA, which was reported by earlier studies (Dricot et al. (2008); Fox et al. (2009); Xu and Biederman (2010)). As we applied spatially non-overlapping stimuli, the OFA, which is sensitive to spatial position, did not get activated. In this study we managed to distinguish face-relevant areas from the perspective of adaptation and found that OFA is only participating in face adaptation if the stimuli are spatially overlapping. This result shows that the OFA is hierarchically subordinate to the FFA, which is already insensitive to actual locations (this finding is in accordance with Haxby et al. (2000) and Ishai (2008)).

In the *third study* (Nagy et al. (2011)) task-relevant activations were measured in the FFA, OFA and LOC for concomitantly presented faces. Our major findings were the following: (1) increasing ratio of faces within the display with four stimuli reduced the BOLD signal in the bilateral FFA and in the right LOC. (2) increasing distance among faces reduced competitive interactions in the FFA; (3) the magnitude of competition depended on the visual hemifield of the stimuli: ipsilateral stimulation reduced the competition effects in the right LOC but increased it in the left LOC.

In the *fourth study* (Nagy et al. (2012a)), we modelled the interactions among

FFA, OFA and LO based on measured functional data (Nagy et al. (2012a)). The main findings are the following: (1) LO is linked directly to the OFA - FFA unit via bidirectional connections; (2) non-face and face inputs are intermixed at the level of occipito-temporal areas and enter the system via LO; (3) face input has a modulatory effect on LO - FFA connection, while object input modulates LO - OFA connection. The present study highlights the role of LO in the core network of face perception. It is highly possible that there is a pathway on which information from the LO goes directly to the FFA. And even if visual information bypasses the OFA, face processing is still possible till a given extent. LO most probably plays a role in structural coding of faces similarly to OFA. Another important conclusion is that visual information is not entirely segregated in this lower level of face perception as both faces and subjects enter the system through the LO.

In conclusion, the present dissertation adds new evidence to the functional specification of face-relevant brain areas. FFA showed adaptation to MFS and the competition among faces also localized in this area, therefore this area is situated on the top of the cortical hierarchy. However, the other well-known face-relevant area, the OFA, is not sensitive to multiple face adaptation and does not participate in sensory competition either. This may further emphasize the position of OFA in the cortical hierarchy, as a subordinate region to FFA.

In our sensory competition study (Nagy et al. (2011)) we found a non-expected decrease in LO activation and by applying effective connectivity analyses we further tested the role of this area in face perception. LO seems to serve as direct input to the FFA, therefore some kind of face processing can be completed in the lack of OFA (For similar conclusions see the neuropsychological case study of Dricot et al., (Dricot et al. (2008))). Implementation of LO in the face-network shows that our knowledge about the face processing brain network is not complete and further studies are needed to explore face-relevant brain areas.

List of publications related to thesis

- Kovács, G., Nagy, K., and Greenlee, M. W. (2011). Sensory competition in the face processing areas of the human brain. In *Perception supplement*, page 40.
- Nagy, K., Greenlee, M. W., and Kovács, G. (2011a). Sensory competition in the face processing areas of the human brain. *PloS One*, 6(9):e24450. PMID: 21912694.
- Nagy, K., Greenlee, M. W., and Kovács, G. (2012a). The lateral occipital cortex in the face perception network: an effective connectivity study. *Frontiers in Psychology*, 3:141. PMID: 22593748.
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- Nagy, K., Zimmer, M., Greenlee, M. W., and Kovács, G. (2012c). Neural correlates

of after-effects caused by adaptation to multiple face displays. *Experimental Brain Research*. PMID: 22673875.

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