



Biological Mechanisms underlying Inter- and Intra-Individual Variability of Face Cognition

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Biological Mechanisms underlying Inter- and Intra-Individual Variability of Face Cognition

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Table of Contents

Abstract.....	1
Zusammenfassung.....	3
Synopsis	5
1 Introduction.....	5
1.1 Aims and Outline of the Present Work	6
1.2 Variability in Face Processing from Behavioral and Neural Perspective	8
1.3 Intra-Subject Variability.....	9
1.4 Neural Bases of Face Processing.....	10
1.5 Methodological Advances in ERP Analysis	12
2 Summary of Studies.....	14
2.1 Study 1: “Dissociating the Influence of Affective Word Content and Cognitive Processing Demands on the Late Positive Potential” (Nowparast Rostami et al., 2016)	14
2.2 Study 2: “COMT Genotype is Differentially Associated with Single Trial Variability of ERPs as a Function of Memory Type.” (Nowparast Rostami et al., submitted).....	15
2.3 Study 3: “Contributions of Structural Encoding and its Top-Down Modulation to Individual Differences in Face and Object Cognition: Evidence from the N1/N170 Components of the Event-Related Brain Potentials” (Nowparast Rostami et al., submitted).....	18
3 General Discussion	22
3.1 Summary of Findings	22
3.2 Limitations.....	24
3.3 Future Outlook	25
3.4 Conclusion.....	27
References.....	29
Original Research Articles.....	61

Abstract

Given the importance of correctly perceiving and remembering faces for successful social interaction, face processing is one of the most widely studied cognitive domain in behavioral, neurophysiological and neuroimaging research, particularly, based on a group-mean approach. However, above mean differences, inter- and intra-individual variability in face processing provide valuable information for investigating the underlying mechanisms and binding the behavioral and neural substrates for better understanding of face processing.

In my dissertation I investigated the biological mechanisms underlying face cognition from an inter- and intra-individual variability perspective at the genetic, neural, and behavioral levels. The neural activities related to face processing are measured by event-related potentials (ERPs) and their trial-by-trial latency variability are estimated using a novel and well-established method, Residue Iteration Decomposition (RIDE).

Study 1 demonstrates the reliability of RIDE in extracting single-trial parameters of the P3b component, which is used in the investigation of the neural basis of intra-subject variability (ISV) in face processing speed in Study 2. In the Study 2, individual differences in ISV of face processing speed, measured at both behavioral and neural levels during a face processing task, are studied in their genetic variation. The results suggest that individual differences in ISV are related not only to the COMT Val¹⁵⁸Met polymorphism, but also to the type of cognitive processing (e.g., memory domain). Moreover, we showed that ISV in reaction time can be partially explained by ISV in the speed of central cognitive processes.

Furthermore, the individual differences approach in Study 3, provided valuable and novel information beyond the common group-mean approach applied in the N1/N170-related research. Based on this approach, not only we could replicate previous findings that the N170 predicts individual differences in face cognition abilities, but also we could decompose individual differences in the N170 into a domain-general and a face-specific part with different predictive powers. Moreover, we showed that top-down modulations on the N170 have separable and qualitatively different relationships to face cognition abilities.

In summary, the integrated results from different studies in my dissertation demonstrate the psychological importance of the information provided by inter- and intra-individual variability in face processing in the investigation of its underlying biological mechanisms.

Zusammenfassung

Die korrekte Wahrnehmung und Erinnerung von Gesichtern ist für eine erfolgreiche soziale Interaktion höchst einschlägig. Somit ist die Gesichtererkennung einer der meist untersuchten Bereiche in den neurokognitiven Wissenschaften. Insbesondere basieren vorhandene Untersuchungen auf Mittelwertvergleiche. Intra- und interindividuelle Unterschiede können jedoch über Mittelwertunterschiede hinaus wertvolle Informationen über die zugrundeliegenden neuronalen Mechanismen der Gesichtererkennung liefern.

In der Arbeit untersuche ich der Gesichtererkennung zugrundeliegenden biologischen Mechanismen auf der genetischen, neuronalen und verhaltensbasierten Ebene. Die neuronale Aktivität wurde mittels ereigniskorrelierter Potenziale (EKPs) untersucht und ihre Latenzvariabilität innerhalb der Person wurde durch eine innovative Methode, Residue Iteration Decomposition (RIDE), gemessen.

Die erste Studie demonstriert die Reliabilität von RIDE für die Extraktion von Einzeltrialparametern der P3b Komponente, welche in der zweiten Studie die Basis für die Untersuchung der Innen-Subjekt-Variabilität (ISV) bei der Geschwindigkeit der Gesichtererkennung bildet. Die zweite Studie untersucht individuelle Unterschiede in ISV in ihrer genetischen Variation, gemessen an der Verhaltens- und neuronalen Ebene während einer Gesichtererkennungsaufgabe. Die Ergebnisse zeigen, dass ISV nicht nur mit dem COMT Val¹⁵⁸Met Polymorphismus zusammenhängt, sondern auch von der geforderten kognitiven Verarbeitung abhängt. Zudem ist die ISV in der Reaktionszeit teilweise durch die ISV in der Geschwindigkeit zentralkognitiver Prozesse erklärbar.

Studie 3 liefert neuartige Informationen für die N1/N170 Forschung. Mit einem differentialpsychologischen Ansatz konnten wir nicht nur vorangegangene Ergebnisse zur Vorhersagekraft der N170 für individuelle Unterschiede in der Gesichtererkennung replizieren, sondern auch die individuellen Unterschiede in der N170 in einen allgemeinen und einen gesichtsspezifischen Teil mit unterschiedlicher Vorhersagekraft zerlegen. Darüber hinaus konnten wir zeigen, dass top-down Modulationen der N170 unterscheidbare und qualitativ unterschiedliche Beziehungen zu Fähigkeiten der Gesichtererkennung aufweisen.

Insgesamt zeigen die integrierten Ergebnisse der Studien meiner Dissertation die psychologische Bedeutsamkeit der intra- und interindividuellen Variabilität in der Gesichtererkennung für die Erforschung der ihr zugrundeliegenden biologischen Mechanismen.

Synopsis

1 Introduction

“Not only our pleasure, our joy and our laughter but also our sorrow, pain, grief, and tears rise from the brain, and the brain alone. With it we think and understand, see and hear, and we discriminate between the ugly and the beautiful, between what is pleasant and what is unpleasant and between good and evil.”

Breedlove, Rosenzweig, and Watson (2007) quoting Hippocrates (about 400 BCE) in Biological Psychology

History tells us that research on brain, behavior and cognition started in antiquity and it has been targeted in many different scientific disciplines. Behavioral and cognitive neuroscience are mostly concerned with the study of the biological mechanisms underlying behavior and cognition at many different levels, such as genes, neurotransmitters, neurons, brain networks, and evolutionary and developmental processes. The very common practice in behavioral and cognitive neuroscience for establishing brain-behavior relationship is linking the *average* brain's structure and functions with behavior and cognition. However, evidence from behavioral and neurobiological studies suggests that performance and neural activity commonly display substantial variability in cognitive functioning within and across individuals. With respect to this matter, researchers are thus increasingly interested in investigating the intra- and inter-individual variability in brain-behavior relationship in order to decipher the neural substrates and mechanisms underlying behavior and cognition (e.g., Braver, Cole, & Yarkoni, 2010; Mohr & Nagel, 2010; Raja Beharelle, Kovačević, McIntosh, & Levine, 2012).

Given the importance of correctly perceiving and remembering faces for successful social interactions, face processing is one of the most widely studied cognitive processes during the last 50 years. Most behavioral, neurophysiological and neuroimaging research on face processing however has been conducted to investigate differences at the average group level between persons or across experimental conditions within persons, in which inter- and intra-individual variance have been treated as 'noise'. Thus, behavioral and neural responses across trials and individuals have been averaged in this research tradition. Although, the findings from the mean level approach have significantly advanced our understanding of the developmental, cognitive, and neural bases of face processing in general, they need to be complemented and extended by valuable information provided by inter- and intra-individual variability in order to better understand deviations from those general trends and possibly their causes. In particular, an inter- and intra-individual differences approach in face processing studies provides a strong potential to associate or dissociate the underlying mechanisms, and bind the behavioral and neural substrates

in order to better understand how this particular human ability is carried out and how it develops (see Yovel, Wilmer, & Duchaine, 2014, for review).

1.1 Aims and Outline of the Present Work

In my dissertation, I started my voyage toward the understanding of the biological mechanisms underlying face cognition, more specifically by combining intra- and inter-individual variability at the level of neural and behavioral measures, a perspective from which the brain-behavior relationship in face cognition has been rarely investigated (section 1.2 and 1.3 provide a relevant brief literature review). Following this approach, I addressed several questions, which have been controversially discussed from several scientific perspectives, such as: Do the neural mechanisms underlying face perception qualitatively differ from the ones underlying object perception? Do higher cognitive functions exert top-down influences on early stages of face and object processing? To which extent neural mechanisms underlying face cognition in early processing stages contribute to individual differences in face cognition abilities? Can such contributions be generalized across non-face stimuli? Which are the neural mechanisms underlying the intra-subject variability in face processing speed? Is intra-subject variability in face processing speed heritable?

To provide an answer to these questions, I measured neural activities during face processing by event-related potentials (ERPs). Because ERPs have an excellent temporal resolution which is vital when the temporal dynamics of the neural activity is of interest, they are a great tool for parameterizing indicators at the neural level. ERPs provide a continuous measure of different stages in cognitive processing, making it possible to determine which stages reflect a specific experimental manipulation (Luck, 2005). Section 1.4 provides a brief introduction about the ERP components reflecting neural bases of face processing.

However, there is at least one main disadvantage in traditional ERP research, which I aimed to step aside in my dissertation. To account for noise in single-trial ERPs most approaches average over a number of trials in a given condition. This technique limits its power by confounding the information about the trial-by-trial variability of the latency and amplitude of ERP components and therefore will lead to severe smearing of the components. This limitation prevents us from reliably investigating the dynamics of cognitive sub-processes. Thus, correlating such smeared ERP components with behavioral outcomes may lead to incorrect conclusions about brain-behavior relationships. A solution to this limitation, which I also applied in my dissertation, has been recently proposed by Ouyang, Herzmann, Zhou, and Sommer (2011). They developed the Residue Iteration Decomposition (RIDE), a method to separate latency-variable from latency-locked component clusters and to estimate latencies and

amplitudes of the cognitive processes in single trials with high precision (more details about the method is provided in section 1.5).

Study 1 included in this dissertation is a methodological demonstration that shows how RIDE provides valuable information regarding intra-subject latency variability of the ERP components and therefore is a sensitive tool to distinguish between neurocognitive sub-processes based on their latency variability on trial-by-trial basis. With this study, I aimed to further evaluate the RIDE method above the work published by Ouyang and colleagues, and validate its sensitivity to capture trial-by-trial latency variability in order to extract reliable single-trial parameters of the P3b component. The estimation of this variability was required for my second work aiming to explain the neural bases of intra-subject variability (ISV) in face cognition speed, which was the focus of Study 2.

In Study 2, individual differences in ISV of face processing speed at behavioral and neural levels have been also assessed with regard to the genetic variation. To this aim, we categorized individuals based on their Val¹⁵⁸Met polymorphism of the catechol-o-methyltransferase (COMT) gene (rs4680), whose association with ISV has been suggested in several studies (e.g., Haraldsson et al., 2010; Stefanis et al., 2005; Saville et al., 2014). As the main part of this study, we applied single-trial analyses on an EEG dataset from face recognition task captured with a face priming paradigm ($N = 91$). Cognitive processing speed in this task was measured at the neural level as latency of the P3b component in each trial using the RIDE method. The relationship between performance speed and P3b latencies on a trial-by-trial basis as well as its association with the COMT Val¹⁵⁸Met polymorphism have been examined by multivariate linear mixed effects modeling.

In Study 3, we focused on the face-selectivity characteristic of N170 component, its contribution to individual differences in face cognition abilities, and the top-down influence of higher order cognitive processes on the early stage of face processing, which has been yet a matter of debate in the literature. In the submitted manuscript, we investigated these questions from an individual differences perspective using structural equation modelling (SEM). To this end, we designed a comprehensive experiment by an orthogonal combination of the content domain (faces vs. objects) and the measurement intention (speed, usually captured in easy task vs. accuracy, measured in difficult task, that cause individual differences in response correctness). This experiment includes separate EEG and psychometric sessions and has been conducted with 211 participants during 9 months (more details about the experiment is provided in section 2.3).

1.2 Variability in Face Processing from Behavioral and Neural Perspective

Inter-individual differences in face recognition have been widely studied on the psychometric (e.g., Megreya & Burton, 2006; Wilhelm et al., 2010; Wilmer et al., 2012) and clinical levels (Duchaine & Nakayama, 2005). It has been revealed that people vary in their face recognition ability in a wide spectrum from very poor face recognition in people with developmental prosopagnosia (Farah, Levinson, & Klein, 1995; Susilo & Duchaine, 2013) to exceptionally good face recognition in super-recognizers who rarely forget a face (Russell, Duchaine, & Nakayama, 2009). Face recognition ability also varies in normal population across age (e.g., Pfützte, Sommer, & Schweinberger, 2002; Schretlen, Pearlson, Anthony, & Yates, 2001; Germine, Duchaine, & Nakayama, 2011; Hildebrandt, Sommer, Herzmann, & Wilhelm, 2010; Hildebrandt, Wilhelm, Schmiedek, Herzmann, & Sommer, 2011), and gender (e.g., Herlitz & Yonker, 2002; Lewin & Herlitz, 2002; Sommer, Hildebrandt, Kunina-Habenicht, Schacht, & Wilhelm, 2013). Thus, the questions arose: What makes individuals unique in their face recognition performance? To answer this question, a number of studies have been trying to understand the cognitive factors determining these individual differences (e.g., Dennett, McKone, Edwards, & Susilo, 2012; Hildebrandt et al., 2011; McGugin, Richler, Herzmann, Speegle, & Gauthier, 2012; Wilhelm et al., 2010; Wilmer et al., 2010). Following this approach, Wilmer et al. (2010; 2012) could dissociate face recognition from more general visual and verbal recognition, suggesting a high degree of specificity in face recognition ability itself and its genetic basis. Moreover, in order to identify possible sources of individual differences in face cognition, Wilhelm et al. (2010) established individual differences factors based on multivariate measurements of face cognition abilities. The task battery was developed by Herzmann, Danthiir, Schacht, Sommer, & Wilhelm (2008) and the measurement domains have been postulated by functional and neuroanatomical models of face cognition (Bruce & Young, 1986), demonstrating the difference between face perception (including the stage of structural encoding) and face memory (including the stages of face recognition units and person identity codes activation). Furthermore, as custom in individual differences research in cognitive abilities two further measurement intentions have been defined for the task construction: processing speed vs. processing accuracy. In the factorial model published by Wilhelm and colleagues (2010), face perception and face memory were differentiable regarding performance accuracy, however individual differences in performance speed were not differentiable for perception and recognition. Thus, individuals who were quick at perceiving faces they were comparably quick in recalling faces from their memory. Therefore, the model included three component abilities of face cognition: Face Perception Accuracy, Face Memory Accuracy, and Face Cognition Speed. These abilities were also distinct from general

cognitive abilities, such as reasoning, working memory, immediate and delayed memory, mental speed, and object cognition. It has been also shown that the specificity of face cognition remains stable as compared with general cognition across the adult life span until old age (Hildebrandt et al., 2011).

Further, available literature revealed considerable variability among persons in the structure of their neural substrates (e.g., Clark et al., 1996; Deffke et al., 2007). In order to better understand the type of face cognition abilities that neural measures of face processing predict, few studies established correlational analysis between behavioral and neural measures across individuals. These studies used ERPs or neuroimaging data (e.g., Alexander et al., 1999; Rotshtein, Geng, Driver, & Dolan, 2007; Schretlen, Pearlson, Anthony, & Yates, 2001; Yovel & Kanwisher, 2005; Herzmann, Kunina, Sommer, & Wilhelm, 2010; Kaltwasser, Hildebrandt, Recio, Wilhelm, & Sommer, 2014). For example, Yovel and Kanwisher (2005) found association between behavioral and fMRI measures of the face inversion effect only in the fusiform face area (FFA), however in mean-level analyses, the face inversion effect was found in both FFA and superior temporal sulcus, as a related face area (STS-FA). Herzmann et al. (2010) and Kaltwasser et al. (2014) reported a moderate correlation between face-related ERP components and multivariate behavioral measures of Face Perception and Face Memory. In these studies, however at the behavioral level, Face Perception and Face Memory were measured in both speed and accuracy tasks, and all ERP components, as typical in ERP research, were measured only in speed tasks. Thus, these measures are informative with respect to the mechanisms underlying processing speed, but possibly not for accuracy. In Study 3 included in my dissertation, we addressed this shortcoming by designing an experiment in which the difficulty of the face and object recognition tasks was manipulated by increasing the memory load in a similar manner like in the psychometric tests already used by Herzmann et al. (2010) and Kaltwasser et al. (2014) (more details on the EEG tasks are provided in section 2.3).

1.3 Intra-Subject Variability

Apart from variability across individuals, intra-subject variability (ISV) of performance has been increasingly recognized as important factor above the average performance. ISV is associated with a number of neurological and neuropsychiatric conditions, such as ADHD (Klein, Wendling, Huettner, Ruder, & Peper, 2006; Kofler et al., 2013; Saville et al., 2015), schizophrenia (Birkett et al., 2007; Rentrop et al., 2010), aging (overview in Schmiedek, Lövdén, & Lindenberger, 2009), and brain injury (Stuss, Murphy, Binns, & Alexander, 2003). Therefore, understanding the neural basis of ISV, which has been rarely addressed in the literature, is crucial and has implications for clinical, developmental, and aging research. In

previous work, the neural mechanisms underlying ISV in performance have been mostly investigated in imaging research (e.g., Walhovd & Fjell, 2007; Bellgrove, Hester, & Garavan, 2004; MacDonald, Li, & Bäckman, 2009) and only very few studies used EEG signals to address this issue (e.g., Segalowitz, Dywan, & Unsal, 1997; Di Russo & Spinelli, 2010; Saville et al., 2011; 2012). Given that the reaction time (RT) variability across trials are usually in the range of several hundred milliseconds, high temporal resolution which is the characteristic of EEG technique is a great advantage for establishing intra-individual brain-behavior relationship.

In previous work, the P3b has been proposed to be a pertinent ERP component associated with ISV in performance. It has been shown that P3b possibly consists of several sub-components representing cognitive processing and response planning (Verleger, Jaśkowski, & Wascher, 2005; Pritchard, Houlihan, & Robinson, 1999). Therefore, in a traditional ERP approach that would average across single trial ERPs, in case of high ISV in RTs, the P3b component can be distorted due to increased trial-by-trial latency variability. Consequently, its relationship to ISV in performance may appear to be an artifact. Saville et al. (2011, 2014) overcome this problem by employing a single-trial approach to ERP analyses. They investigated intra-individual brain-behavior relationship by correlating P3b latency and amplitude measures extracted in each trial to single-trial RTs. However, principal component analysis (PCA) and a filter-based method used in this study for single-trial ERP estimation do not differentiate between sub-components reflecting cognitive and motor processes in the latency estimation. Thus, contribution of response selection- or motor processes-related sub-components to the evaluation of ISV in performance may result in a high correlation which cannot be interpreted as relationship between cognitive processes reflected in P3b and behavior.

Thus, in Study 2 we went one step further by using RIDE method to investigate neural underpinning of face processing speed from the viewpoint of intra-subject variability. As we showed in Study 1, the strength of the RIDE method in this case is that it can separate the sub-components reflecting cognitive processes with variable single-trial latencies from the sub-components reflecting motor processes with latencies locked to the RTs and the ones reflecting stimulus processes with latencies locked to the stimuli. Thus, this method provides an opportunity to characterize individual differences in the trial-by-trial variability of cognitive processes speed excluding motor processes.

1.4 Neural Bases of Face Processing

As compared with hemodynamic methods, such as fMRI and PET, which are limited by the slow speed of the BOLD response, ERPs provide an excellent temporal resolution which is vital to research questions related to temporal dynamics of the neural activity. ERP components as

neurocognitive indicators carry information in their latency and amplitude measures, reflecting the temporal dynamics and efficiency or neural effort invested for cognitive processing, respectively. In ERP research several components have been defined as reflecting specific neurocognitive sub-processes that are functionally associated with different stages involved in face recognition according to the Bruce and Young model (1986), which is the most widely cited functional face processing model (see Estudillo, 2012; Herzmann & Sommer, 2007). The first stage in this model is called *structural encoding* including two separate processes: *View-centered description*, reflected in the P100 component and *expression-independent description*, reflected in N170 component. The **P100** is the increased occipital positivity generated in extrastriate visual cortex and observed about 100 ms after stimulus onset. This component reflects pictorial encoding, that is, processing of domain-general, low-level visual stimulus features (e.g., Doi, Sawada, & Masataka, 2007). The **N170**, known as face-sensitive component and characterized by a negative peak around 170 ms after stimulus onset and maximal in inferior occipitotemporal cortex, is larger for faces as compared to those elicited by other non-face visual stimuli like houses (e.g., Bentin, 1996; Eimer, 2011). This component reflects configural encoding of facial features, namely, holistic processing of faces (e.g., Rossion & Jacques, 2008; Eimer, Gosling, Nicholas, & Kiss, 2011).

The next processing stage after expression-independent description in structural encoding module involves activation of *face recognition units* (FRU). The face being observed can be recognized if the corresponding node in FRU reaches the threshold level of activation. The **N250r/ERE** (early repetition effect) component seems to be related to the activation of FRU, reflecting activation of the stored knowledge about structure of faces in long-term memory (see Schweinberger, 2011, for review). This component is sensitive to stimulus familiarity and is absent or smaller for unfamiliar faces (Herzmann & Sommer, 2010; Schweinberger, Pickering, Burton, & Kaufmann, 2002). The ERE occurs as a negativity for primed relative to unprimed faces, around 250-350 ms after stimulus onset and over inferior temporal sites.

When the face is recognized, as the next stage of processing, *person identity nodes* (PIN) receives input from the FRU and provides semantic information about that person. There is two-way interaction between FRU and PIN in this model which can explain the repetition effect observed in repetition priming paradigm in face recognition tasks. The **N400/LRE** (late repetition effect) component was reported to be stronger for faces presented with additional semantic knowledge about the person (Paller, Gonsalves, Grabowecky, Bozic, & Yamada, 2000), thus reflects semantic memory codes stored in PIN. This component is also larger for familiar than for unfamiliar faces (Paller, Gonsalves, Grabowecky, Bozic, & Yamada, 2000; Schweinberger,

Pickering, Burton, & Kaufmann, 2002). The LRE, as increased central-parietal positivity for primed relative to unprimed familiar faces occurs between 350 and 600 ms after stimulus onset.

Besides, further components have been specified as functional, neurocognitive sub-processes associated with old/new effects in recognition paradigms (Yonelinas, 2002). Although these components are not directly related to face processing mechanisms, they can be informative about the processes underlying face retrieval. The old/new effect in face recognition (e.g., Johansson, Mecklinger, & Treese, 2004; Nessler, Mecklinger, & Penny, 2005), characterized by a larger positivity for old as compared to new faces in ERP studies, is reflected in the **FN400**, an early anterior effect around 300-500 ms, and in the late positive component (LPC), a late posterior effect around 400-800 ms. Both of these components are related to explicit recognition memory (Friedman & Johnson, 2000). Based on dual-process theory, recognition memory can be dissociated to two distinct memory processes: Recollection, a process involving retrieval of specific details, and familiarity, as a feeling of knowing in the absence of source information (Yonelinas, Otten, Shaw, & Rugg, 2005). It has been suggested that FN400 and LPC are associated with familiarity and recollection processes, respectively (e.g., Curran, 2000; Wolk et al., 2006).

1.5 Methodological Advances in ERP Analysis

ERPs are ideally suited for studying the temporal dynamics of the mental processes that occur between stimulus and response. High temporal resolution in ERPs allows to isolate different cognitive processes. However, in case of strong response variability, averaging trials used in ERPs will lead to mixing several ERP components together. For example, a component related to motor process in a trial with a short RT may combine with a component reflecting perception or decision making in a trial with large RT. This is crucial because it becomes difficult to reliably investigate the temporal dynamics of neural sub-processes which is a key to study brain-behavior relationship based on EEG data. RIDE is a new method to overcome the smearing and mixing problem due to the latency variability of the sub-processes and corresponding ERP components by estimating component latencies in each trial and accordingly separating different ERP component clusters based on their trial-by-trial latency variability (Ouyang et al., 2011; Ouyang, Sommer, & Zhou, 2015a; 2015b). RIDE decomposes ERPs into a stimulus-locked, a response-locked, and an intermediate component cluster that includes all components which have no explicit latency information (S-, R-, and C-component clusters, respectively). Each cluster may include several ERP components with distinct functional significance, but with similar time-locking pattern. RIDE also provides waveforms and topographies of each separated component cluster using spatiotemporal cross-correlation. Similar methods exist, however they do not allow

assessing the topographical evolution because of estimating the latencies of different channels independently (Takeda, Sato, Yamanaka, Nozaki, & Yamamoto, 2010; Takeda, Yamanaka, & Yamamoto, 2008). Moreover, RIDE can reliably estimate the single-trial amplitude and latency measures of each component cluster, providing an excellent opportunity to characterize individual differences in the trial-by-trial variability of ERP components at each processing step. The advantage of RIDE as compared with other temporal decomposition methods is that (1) it can separate components with or without explicit latency information, allowing application to data from tasks without responses like reading (Ouyang, Schacht, Zhou, & Sommer, 2013). (2) It avoids slow wave amplification and distortion by using median rather than L2-norm minimization used by Hansen (1983) and Takeda et al. (2010). (3) The refinement algorithms used by RIDE lead to more psychologically relevant outcomes. Since all cognitive experiments show RT variability and thus smearing effects on conventional average ERPs, this method has great potential for numerous applications in studying the mechanism of cognitive sub-processes and response variability.

2 Summary of Studies

2.1 Study 1: “Dissociating the Influence of Affective Word Content and Cognitive Processing Demands on the Late Positive Potential” (Nowparast Rostami et al., 2016)

During the last 20 years, there were many arguments on a distinction of emotion processes from other cognitive processes (for an overview, see Eder, Hommel, & De Houwer, 2007; Cacioppo & Berntson, 2007). To operationally capture the degree of distinctiveness of emotion processing, the late positive potential (LPP) has been recently considered a relevant component characterizing affective processing (see Weinberg, Ferri, & Hajcak, 2013, for review). On the other hand, the P3b component has been a prominent measure to study cognitive processes for decades (see Eder et al., 2007, for review), thus it has been considered a relevant measure for comparing cognitive with affective processing. Both LPP and P3b are ERP components with an increased centroparietal positivity, starting around 300 ms after stimulus onset and lasting for several hundred milliseconds (e.g., Cuthbert, Schupp, Bradley, Birbaumer, & Lang 2000). Since these two components are overlapping in terms of latencies and are similar in terms of scalp topographies, the question arises whether they represent the same or distinct sub-components. Some studies support functional similarity of LPP and P3b, with the idea that they reflect the same processes if they are similarly modulated by the same variables, such as attention (e.g., Schupp et al., 2007; Schacht & Sommer, 2009). On the other hand, some other studies assessing functional relationship between these two components argued against functional similarity of LPP and P3b by showing they are not modulated similarly by the same variables (e.g., Cuthbert et al., 2000; Codispoti, Ferrari, & Bradley, 2006). Moreover, using spatiotemporal PCA, Matsuda and Nittono (2014) could decompose LPP into sub-components with different topographies which are differentially reflecting affective content and cognitive processing demands.

In Study 1, we investigated whether the underlying neural processes associated with the affective content (LPP) and with the cognitive processing demands (P3b) are equivalent or represent distinct sub-components. To this aim, we used information about trial-by-trial latency-variability characteristic of each component extracted by the RIDE method and topographical comparison technique. We applied RIDE on the EEG data from twenty-three healthy young participants taken from a study by Bayer, Sommer, and Schacht (2012). In this study the task was either passive reading of high/low arousing words with positive/neutral/negative valence or a lexical decision task (LDT) with the same words as targets. In this experiment, the emotion (both arousal and valence) and task effects were considered as a measure of affective processing (LPP) and cognitive processing demands (P3b), respectively. The temporal features of the LPP and the P3b were assessed by decomposing ERPs in each condition into stimulus-locked (S), latency-

variable (C), and response-locked (R) component clusters according to their latency variability in trial-by-trial basis. In addition, topographies of both components were compared using non-parametric permutation test, following the procedure described by Murray, Brunet, and Michel (2008). After RIDE decomposition, the arousal and valence effects (LPP) appeared to be significant only in S component cluster and the task effect was more pronounced in latency-variable C component cluster. This shows that the processes underlying LPP are rather directly coupled to the stimuli and the ones underlying P3b appeared to be more temporally independent. Additionally, in spite of the relative similarity between the topographies related to LPP and P3b, statistical comparisons of the topographies indicated that they are significantly different which is consistent with the findings reported by Matsuda and Nittono (2014). The arousal and valence effects (LPP) showed mainly central positivity, whereas the task effect (P3b) was mostly pronounced at centroparietal electrode sites. The difference in topographies suggests that at least partially different neural generators are involved in emotion and task effects. That is, the LPP elicited by affective content and the P3b elicited by cognitive processing demands are not reflecting exactly the same sub-processes and thus they can be assumed to be two sub-components of the late positivity.

In conclusion, RIDE decomposition technique and topographical comparisons used in Study 1 showed that late positive components reflecting affective processing (defined as LPP) and cognitive processing demands (defined as P3b) are dissociable in terms of temporal features and neural generators, thus they are at least partially influenced by different sub-processes carried out in the brain.

2.2 Study 2: “COMT Genotype is Differentially Associated with Single Trial Variability of ERPs as a Function of Memory Type.” (Nowparast Rostami et al., submitted)

ISV in performance is a promising endophenotype for several psychiatric conditions, such as schizophrenia (Rentrop et al., 2010) and ADHD (Klein et al., 2006; Kofler et al., 2013; Saville et al., 2015). Evidence from psychopharmacology and molecular genetics suggests a link between ISV and the status of the catecholaminergic system, which is a neurotransmitter system involved in numerous cortical functions, such as memory, learning, and behavior, as well as several neurodegenerative disorders and psychiatric conditions, such as Alzheimer’s disease, Parkinson, and Schizophrenia. In a molecular genetic approach, the Val¹⁵⁸Met polymorphism (rs4680) of the COMT gene can be studied as a factor to measure catecholamine functioning. The COMT gene regulates the production of the enzyme catechol-o-methyltransferase that deactivates catecholamines, such as dopamine, epinephrine, and norepinephrine by methylation. It is particularly essential for deactivation of dopamine in the prefrontal cortex (PFC), influencing the

sustained activity in PFC neurons and thus influencing stability and accuracy of cognitive performance. VAL¹⁵⁸ homozygotes deactivate dopamine 3-4 times faster than MET¹⁵⁸ homozygotes, which results in decreased dopamine availability in PFC and shorter impact of dopamine in the synaptic cleft.

Because of the contradictory results of the relationship between ISV in performance and COMT polymorphism across studies (e.g., Haraldsson et al., 2010; Stefanis et al., 2005), it has been suggested that this relationship may depend on the type of cognitive demands (Cools & D'Esposito, 2011). ISV in performance can be related to different stages of cognitive processing. Saville et al. (2014) studied the effect of the COMT Val¹⁵⁸Met polymorphism on a specific stage of cognitive processes by measuring single-trial P3b latencies in a set of n-back tasks. In this study the authors used a P3b estimation approach in single trials that has been suggested by Saville et al. (2011), a trial-base peak picking method using data aggregation across electrodes and filtering. As a result of this study, Val⁺ genotypes were associated with lower ISV in both RTs and P3b latencies, similar to the findings of Haraldsson et al. (2010), but at variance with those of Stefanis et al. (2005).

In Study 2, first we replicated the findings of Saville et al. (2014) by reanalyzing their data using an alternative single-trial analysis method, the RIDE described above. By applying RIDE we could measure ISV of cognitive processing speed after excluding overlapped motor-related sub-components with latencies locked to the RTs. Results showed that increased variability in C latencies was associated with increased number of Met alleles.

Second, we investigated whether individual differences in ISV found in working memory tasks in Saville et al. (2014) would replicate on a different task, recruiting different type of memory. Using RIDE, single-trial analysis has been applied on an EEG dataset captured with a face recognition task with a priming paradigm ($N = 91$). This dataset was reported previously in Kaltwasser et al. (2014) for an independent research question. ISV of cognitive processing speed at the neural level has been measured as trial-by-trial variability in the latencies of the C component identified by RIDE. Then, individual differences in ISV of face processing speed at behavioral and neural levels have been assessed depending on the COMT genotype. The results from face recognition tasks showed different association between the COMT genotype and C latency variability in familiar vs. unfamiliar task conditions. The trial-by-trial variability of C latency in individuals with more copies of the Val allele was significantly larger in unfamiliar than in familiar face conditions. In contrast, Met/Met carriers showed no significant difference in their variability of recognizing familiar vs. unfamiliar faces. Moreover, all individuals across

genotype groups showed similar ISV in C latency in familiar face recognition as compared with unfamiliar face recognition.

The results related to ISV at the neural level were supported with a very similar pattern when considering ISV at the behavioral level (ISV in RTs). These findings suggest that individuals with more copies of Val allele are less stable (more flexible) than Met/Met carriers in different task conditions which require a different type of memory access – in our case, simple matching of memory representations in familiar faces condition vs. memory search requested in the unfamiliar faces condition. This is consistent with studies suggesting that Val alleles are associated with increased cognitive flexibility and Met alleles with increased cognitive stability (e.g., Markant, Cicchetti, Hetzel, & Thomas, 2014; Nolan, Bilder, Lachman, & Volavka, 2004). Furthermore, comparing the results from face recognition tasks representing a specific form of secondary memory with the ones from n-back tasks as recognition working memory tasks suggests the association of COMT genotype to ISV at both neural and behavioral levels to be a function of memory type.

Besides, we also investigated to which extent ISV at the level of behavior can be explained by ISV measured at the neural level. The relationship between performance speed and C latencies on a trial-by-trial basis, as well as the effect of COMT on it have been examined by multivariate linear mixed effects modeling in both datasets. In both samples, C latency showed substantial power on predicting RT on the trial-by-trial level. In the dataset from the n-back tasks, the latency of the central cognitive processes was less predictive of RT in Met/Met carriers, who were more variable at both electrophysiological and behavioral levels, than in Val allele carriers. However, in the dataset captured by the face recognition tasks, in familiar conditions, showing less ISV than the unfamiliar conditions at both the electrophysiological and behavioral levels, the C latency turned out to be a better predictor of RT than in the unfamiliar conditions. In this dataset COMT did not modulate the predictive power of C latency. The findings in both datasets suggest that larger ISV in RT represents increased variability in several neurocognitive sub-processes as measured by ERPs.

In conclusion, Study 2 provides evidence suggesting that individual differences in intra-subject variability do not only depend on the COMT genotype, but also COMT effects on ISV depend on the type of cognitive processing (e.g., memory domain). Moreover, we could show that ISV in RT can be to some extent explained by C latency variability which is capturing the speed of central cognitive processes on a trial-by-trial basis.

2.3 Study 3: “Contributions of Structural Encoding and its Top-Down Modulation to Individual Differences in Face and Object Cognition: Evidence from the N1/N170 Components of the Event-Related Brain Potentials” (Nowparast Rostami et al., submitted)

From several scientific perspectives, it has been a controversial issue for long that whether the neural mechanisms underlying face cognition differ substantially from the ones underlying non-face object cognition. For example, evidence from people with prosopagnosia with an isolated ability in recognizing faces but not non-face objects suggests distinct mechanism involved in face recognition (see Young, 2011, for review). In contrast to the evidence supporting domain-specificity of face cognition (see Kanwisher & Yovel, 2006, for review), some evidence supports domain-general hypothesis, postulating that the same mechanism underlies both face and non-face object processing. For example, the expertise hypothesis (Diamond & Carrey, 1986) suggests that the specific mechanisms underlying face processing are engaged in processing of any kinds of non-face visual stimuli of expertise, like cars, birds, etc (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Gauthier, Skudlarski, Gore, & Anderson, 2000; Xu, 2005).

From a neurophysiological perspective, which is particularly important in the context of this study, it has been shown that the N170 component can be considered a face-specific component because of being remarkably larger in its amplitude during the processing of faces than for other types of visual stimuli (e.g., Bentin, Allison, Puce, Perez, & McCarthy, 1996; Jeffreys, 1996; Eimer & McCarthy, 1999; Eimer, 2011). However, the N170 has been considered to belong to N1 component family elicited in response to non-face visual stimuli. Thus, it is unclear whether the neural processes underlying these two components are qualitatively different (arise from different or partially different processes) or quantitatively different (arise from the same processes but with different intensity). In a differential approach, correlational pattern of the measured variables in multiple experimental conditions can help to distinguish between these two alternatives. In such an approach, if pattern of correlations changes as a consequence of experimental manipulations, it indicates that they induce different mixture of sources or processes. On the other hand, if the correlational pattern does not change, it indicates that more or less of the same processes are involved in both control and experimental conditions (Oberauer, Wilhelm, & Schmiedek, 2005). Therefore, beside the research based on a group-mean approach, some studies investigated neural mechanisms underlying face processing from individual differences perspective, where variation across individuals has been treated as valuable information (see Yovel, Wilmer, & Duchaine, 2014, for review). A brief introduction about some of these studies which are relevant to Study 3 and their limitations is provided in section 1.2.

In Study 3, by orthogonally combining the content domain (faces vs. houses) and task difficulty (easy/speed vs. difficult/accuracy) in both the EEG experiment and the psychometric task battery, we aimed to investigate (1) whether the neural mechanisms underlying face cognition abilities are qualitatively different from the mechanisms underlying object cognition abilities and whether difficulty of the task induces additional sources or processes in the early stage of face and object cognition. (2) Whether the relationship between N170 latency and face cognition abilities found in Herzmann et al. (2010) and Kaltwasser et al. (2014) are face-specific or can be generalized to object domain. (3) Whether this relationship can be influenced by task difficulty, as a reflection of top-down effect on early stage of face processing. To these aims, we collected psychometric and EEG data from 211 participants in two independent sessions (EEG vs. psychometrics). In the psychometric test battery, including multiple tasks, we orthogonally combined speed (easy) and accuracy (difficult) tasks for both face and object perception and memory, aiming to capture the accuracy and speed of face perception (FP), face memory (FM), object perception (OP), and object memory (OM). In the EEG experiment, content domain (faces vs. houses) and task demand (low memory load/easy vs. high memory load/difficult) were orthogonally manipulated within recognition tasks based on a priming paradigm. After pre-processing of the data, we analyzed each dataset and the brain-behavior relationship from individual differences perspective using SEMs. First, we established the best fitting psychometric models, separately on speed- and accuracy-related indicators of FP, FM, OP, and OM in order to study the uniqueness of the processes underlying face cognition as compared with object cognition abilities at the behavioral level. The best fitting speed-related model provided evidence for no distinction between the processes underlying FP, FM, OP, and OM in easy tasks. Moreover, the best fitting accuracy-related model revealed that the accuracy of face perception, face memory, and object memory are specific abilities above general object perception accuracy; that is, in difficult tasks both domain (face vs. object) and processes (perception vs. memory) are distinct. The findings at the behavioral level are consistent with the findings in previous work (Hildebrandt et al., 2010; 2011; 2012; 2013; Wilhelm et al., 2010).

Second, at the electrophysiological level, we measured the N1/N170 latencies and amplitudes in all four conditions (primed-familiar, unprimed-familiar, primed-unfamiliar, and unprimed-unfamiliar) of all four recognition tasks (face-easy, face-difficult, object-easy, object-difficult). Then, we established the measurement models on the N1/N170 indicators separately for latencies and amplitudes. Both best-fitting models of the N1/N170 latency and amplitude involved a general factor, accounting for the common variance across all tasks, and an additional specific factor, accounting for the common variance among the variables derived only from the

face cognition tasks. The face-specific factor indicates additional sources or processes underlying face cognition which are not involved in object cognition. This model revealed that the N170 to faces reflects the processes composed of a face-specific part and a part which is the same as the processes underlying object cognition in the early stage reflected in the N1 component. In addition to the specific face-related variance in the N170 latency and amplitude, the models indicated another specific variance above the general factor which were shared only among the indicators from face or object recognition task with high memory load. These specific factors indicate that high memory load or difficulty of the task induces additional processes that are qualitatively different from the set of processes needed for processing face and object stimuli when the task is easy in terms of memory load. This finding supports a top-down influence by higher-order cognitive processes on both N1 and face-specific part of the N170 components.

Third, in order to measure the contributions of the N1/N170 latency and amplitude to individual differences in speed and accuracy of face and object cognition, the regression weights between the established N1/N170 factors and the latent variables obtained from behavioral data were calculated, using SEMs. These SEM models revealed that, (1) individual differences in the latency of the face-specific part of the N170 component contributed negatively to individual differences in the accuracy of FP, FM, and OM. Thus, individuals with faster structural encoding of faces are more accurate in perceiving faces and memorizing both faces and objects. This finding shows that the latency of only face-specific part of the N170 component is to some extent in charge of the accuracy in perceiving and memorizing faces and this relationship cannot be generalized to the N1 component and object cognition abilities. (2) In contrast to the N170 latency and FP accuracy relationship in easy task, individual differences in the latency of the face-specific part of the N170 in difficult conditions contributed *positively* to FP accuracy. Thus, those individuals who slow down their structural encoding processes under accuracy demands, benefit in perceiving faces. This can be argued as a top-down effect on structural encoding of faces when task is difficult. (3) Individual differences in the face-specific part of the N170 amplitude in difficult conditions contributed positively to individual differences in the accuracy of FP, FM, and OM. It suggests that individuals with stronger neural activity during structural encoding of faces under accuracy demands are more accurate in face perception and memory, as well as object memory. The stronger involvement of the neural activity under difficult condition suggests a top-down effect on the structural encoding of faces when the task is difficult. This shows the benefit of the top-down effects for better face recognition performance. (4) In contrast to the positive relationship of the face-specific N170 amplitude and FP accuracy in difficult task, individual differences in N1 amplitude indicating processes underlying object perception in

difficult conditions were *negatively* correlated with general factor accounting for the object perception-related variance. That is, individuals who decrease their N1 amplitude in perceiving objects under accuracy demands are more accurate in object perception. This contrast may indicate the dissociation of top-down modulation on N1 and face-specific N170 in difficult conditions.

In conclusion, Study 3 provided some evidence suggesting that (1) the processes underlying face cognition are qualitatively different from the ones underlying object cognition. (2) The difficulty of the task influences the processes in the early stages of face and object cognition. (3) The latency of the face-specific N170 and the amplitude of both N1 and N170 can to some extent explain individual differences in face and object recognition abilities.

3 General Discussion

3.1 Summary of Findings

Aiming to contribute with a better understanding of the biological mechanisms underlying inter- and intra-individual differences in face cognition, the present dissertation investigated the variability in face processing from neural, behavioral, and genetic perspectives. At the neural level, the indicators of face processing are measured in ERPs because of its high temporal resolution. Out of all ERP components indicating neurocognitive sub-processes associated with different stages involved in face recognition (see section 1.4), the N170 reflecting the structural encoding of faces and the late positive component associated with old/new effect in face recognition were of interest in this dissertation. However, ERP components are well-suited for studying the temporal dynamics, averaging across trials in a traditional ERP approach leads to mixing several ERP components especially in late time windows where the latencies of components across trials are more variable (see section 1.5). This problem could prevent us from reliably measuring the late positive component (P3b) which was the component of interest in Study 2. Therefore, the first research question addressed in this dissertation concerned about the smearing and mixing problem due to the latency variability of especially late sub-processes and corresponding ERP sub-components. By applying the RIDE method in Study 1, we could dissociate the late positive sub-components associated with emotion processing (LPP) and cognitive processing demands (P3b) based on their trial-by-trial latency variability features, although they appear to be similar or even equivalent in terms of time course and topography in conventional average ERP analysis. Our finding in this study confirmed that RIDE can separate the latency-variable sub-components reflecting cognitive processes from the stimulus- and response-locked sub-components, respectively, reflecting stimulus and motor processes. Thus, we could demonstrate that the information about trial-by-trial latency variability of the ERP components provided by RIDE makes it a proper method to extract reliable single-trial parameters of the latency-variable late positive sub-components associated only with cognitive processes. This information was required in Study 2 in which we addressed neural and genetic basis of individual differences in ISV of face cognition speed. In this study we showed that ISV of face cognition speed in both RT and C latency (equivalent to latency-variable sub-components of the late positive component) is stable in Met/Met carriers but depends on the familiarity of the faces in Val/Val carriers, showing larger ISV in recognizing unfamiliar faces than familiar ones. Moreover, ISV in RT and C latency was similar for all individuals across genotype groups in familiar as compared with unfamiliar face recognition. The reason that Val/Val carriers are more variable in case of unfamiliar face recognition as compared with Met/Met carriers, can be

explained by their personality. In many studies the association between COMT and personality traits has been proved (see Montag, Jurkiewicz, & Reuter, 2012, for review). For example, it has been shown that Val/Val genotype is associated with *novelty seeking* (e.g., Reuter & Henning, 2005; Tsai, Hong, Yu, & Chen, 2004) which is a personality trait associated with avoidance of frustration and exploratory activity in response to novel stimulation (Cloninger, Svrakic, and Przybeck, 1993). Hence, it can be speculated that in case of unfamiliar face recognition which leads to exhaustive search in the memory (FRU), if the target face is not distinctive enough from learned faces to be recognized quickly as unfamiliar face, Val/Val carriers tend to search more in FRU to be sure that there is no matched structural code and Met/Met carriers tend to guess instead of searching through the whole stored structural codes. Since some unfamiliar faces are more distinctive and need less searching time and some others need longer search through the FRU, not being frustrated will definitely result in larger ISV than just using guessing strategy. Moreover, the brain-behavior relationship regarding the intra-subject variability in face cognition speed in this study showed that face cognition speed in performance can be to some extent predicted by C latency on a trial-by-trial basis. Besides, combining the findings in this study with the replication of findings from Saville et al. (2014), as explained briefly in summary of Study 2, we could provide some evidence suggesting that individual differences in ISV not only can be related to the COMT genotype, but also can be related to the type of cognitive processing (e.g., memory domain).

Besides, we addressed neural mechanisms underlying face processing from individual differences perspective in Study 3. This study involves a well-structured experimental design in both EEG and psychometric levels, a large number of sample size in order to bring up the statistical power, and advanced statistics applied for modelling the data. The differential approach considered in this study, by using nested SEMs, provided a golden opportunity to address the uniqueness of the processes underlying face cognition as compared with object cognition in early stages of processing and the influence of task difficulty on them. In this study at the behavioral level and in line with the findings in previous studies, we showed that the same processes underlie the speed of face and object processing in both perception and memory when the tasks are easy and in contrast, in difficult tasks different processes are in charge of the accuracy in face perception, face memory, object perception, and object memory. At the neurophysiological level, we indicated that the N170 to faces reflects the processes which are partly the same as the processes underlying object cognition in the early stages as reflected in the N1 and partly specific to faces which are qualitatively different from the object-related processes. In addition, in both latency and amplitude measures, we showed that the difficulty of the task induces additional

sources or processes in the early stage of both face (N170) and object processing (N1), suggesting top-down effect on the N170 and N1 components. At the level of brain-behavior relationship, we showed that the face-specific part of the N170 latency can be to some extent predictive of the individual differences in face and object recognition abilities and this brain-behavior relationship cannot be generalized to the N1 component. This supports the qualitative difference between the processes which are reflected in the face-specific part of the N170 and in the N1. Moreover, we showed that under the accuracy demands in difficult tasks the pattern of the relationship between the latency and amplitude of N1/N170 and face and object cognition abilities changes. As another evidence, this also supports the top-down effect on the early stage of stimulus processing.

3.2 Limitations

Though the present dissertation extended our knowledge about some specific mechanisms underlying face cognition abilities, there were some limitations which are mentioned in this section and solutions are suggested for improvements in following studies.

In Study 2, first, the relatively small and unequal number of sample size in each genotype group can be considered a main shortcoming which limits the power of linear mixed effects models applied in this study. Second, the sex difference were ignored in this study because of the limited number of observations in the samples, however it has been previously shown in the literature that, for instance, the association between COMT and personality which can explain our findings in this study is strongly influenced by sex (Chen et al., 2011). Third, regarding the brain-behavior relationship in face cognition speed, both neural and behavioral measurements have been collected in the same experiment. In future work, it is better to go beyond this approach that intrinsically contains statistical dependency between the measurements. The possible task-related correlations due to statistical dependency can be avoided by estimating relationships between ISV in neurocognitive and behavioral indicators as latent constructs measured in independent experimental tasks. Forth, in order to investigate whether the neural and genetic bases of individual differences in ISV of face cognition speed are face-specific or could be generalized to other content, the experiment should be extended to object recognition tasks preferably at both EEG and psychometric levels. A replication of Study 2 using the dataset collected in the Study 3 can potentially overcome the limitations mentioned above, because it includes (1) a large number of observations included in the sample, (2) face and object recognition tasks in both EEG experiment and psychometric test battery measured in independent sessions, and (3) saliva-derived genomic DNA samples which can be used to define the genotype of COMT Val¹⁵⁸Met polymorphism in each individual.

In Study 3, the different size of face and house stimuli used in the experiment, in the first glance could be considered as a limitation to address the specificity of the neural mechanism underlying face cognition in early stage due to the fact that early visual components are affected by low-level visual features, such as size of the stimuli. However, we believe that the difference in low-level features, although important in studies pursuing an experimental (mean differences) approach, does not affect the correlational structure, the approach which has been applied in the Study 3. The main limitation of Study 3 is that the source of the top-down effect on N170 and N1 is not clear. Based on the current experimental design we cannot conclude the top-down effect is resulted from the high memory load per se, difficulty of the task due to high memory load, or the additional attention paid to the stimuli implicitly under higher cognitive demand in difficult condition. Furthermore, the specificity of the cognitive and neural mechanisms underlying face cognition within neurophysiological research was mainly challenged by the expertise point of view. Thus, it would be an important contribution to the specificity debate if we could investigate the specificity of face processing also in experts of houses, as representative of objects in this study, by comparing their ability structure of face vs. object cognition with the structure established for “only” face experts.

3.3 Future Outlook

The EEG experiment and psychometric test battery mentioned in Study 3 were designed and conducted to address several questions in relatively longer-term. The results obtained and presented here have addressed some of the questions (see Study 3) and a few further works on this dataset will be done/are ongoing as explained in the following paragraphs.

Neurocognitive mechanisms underlying speed and accuracy of face and object processing

The dichotomy between domain-general abilities representing mental processing speed and domain-specific abilities of face and object cognition accuracy and the neurocognitive mechanisms underlying speed and accuracy of face and object cognition which have been addressed in Study 3 was limited only to the N170 component known to indicate part of perceptual processes. Thus, the diligent approach applied in this study can be extended to other ERP components indicating central (e.g., memory, decision, and response selection) and motor processes in face and object cognition. To this aim, the power of RIDE method can be also employed to enhance the measurement models of ERP indicators by parameterizing ERP components that are not smeared due to latency variability.

In addition, assuming that the total variance in performance speed and accuracy across subjects is mostly driven from the variance in perception, central processing, and motor

processing, we will investigate whether the contribution of central processing to performance variance enhances in accuracy as compared with speed tasks. In order to test this assumption we will use a latent variable approach for modeling behavioral outcomes and ERPs and relate them to each other in SEMs. Moreover, we will ask whether individual differences in the accuracy of face and object perception and recognition are differentially related to the central processes measured during performing accuracy tasks within the same vs. non-corresponding content domains.

The relationship between pre-stimulus EEG and face and object cognition abilities

In the current dissertation, the neurocognitive mechanisms underlying inter-and intra-individual variability in face and object cognition have been investigated from a post-stimulus brain activity perspective. However, it is unclear whether the variability in stimulus processing could be explained by the fluctuation in pre-stimulus activity and whether the association of the N170 component and face and object recognition abilities found in Study 3 is a function of pre-stimulus processing. Thus, we wish to investigate whether the variation of pre-stimulus activity explains the variability of the ERP components and whether it has any impact on face and object recognition abilities.

Gender effect on the N170 component

In Study 3, the conclusions regarding domain specificity and difficulty effects on the N170 amplitude and latency and their relationship with face and object cognition abilities were made from an individual differences perspective, but without considering gender differences as an independent factor. However, the superiority of women in face cognition has been already shown in several studies (e.g., Sommer et al., 2013). Therefore, there is need for extension of the models reported in Study 3 by adding the gender as a factor to investigate whether there is a gender difference in structural analysis to faces and if yes, whether it can explain the gender difference in face cognition abilities.

Priming and familiarity effect in face cognition

It has been a controversial issue whether the priming effect is just a latency shift of primed vs. unprimed condition or it is showing two different underlying processes. The large dataset and the experimental design including priming paradigm used in Study 3 provides the opportunity to investigate this issue in both face and object recognition. Using RIDE method, we can explore the neural underpinning of priming effect in the central processes after excluding the response-related processes.

3.4 Conclusion

The present dissertation helped to elucidate the biological mechanisms underlying face cognition by investigating inter- and intra-individual variability at the neural, behavioral, and genetic levels. We showed that (1) the neural mechanisms underlying face perception qualitatively differ from the ones underlying object perception. (2) Memory load as a higher cognitive function exert top-down influences on early stage of face and object processing, reflected in N1 and N170 components. (3) The neural mechanisms underlying face cognition in early processing stages, reflected in N170, contribute to the individual differences in face cognition abilities. (4) These contributions are specific to faces and cannot be generalized across non-face stimuli. (5) Intra-subject variability in face processing speed is heritable. (6) Individual differences in ISV at both behavioral and neural levels are related not only to the COMT Val¹⁵⁸Met polymorphism, but also to the type of cognitive processing (e.g., memory domain). (7) ISV in face processing speed can be partially explained by ISV in the speed of central cognitive processes, reflected in P3b component.

In conclusion, the integrated results from different studies in my dissertation demonstrate the psychological importance of the information provided by inter- and intra-individual variability in face and object processing for investigating the underlying biological mechanisms and the brain-behavior relationship in order to better understand how this particular human ability is carried out and how it develops.

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Original Research Articles

- I. Nowparast Rostami, H., Ouyang, G., Bayer, M., Schacht, A., Zhou, C., & Sommer, W. (2015). Dissociating the influence of affective word content and cognitive processing demands on the late positive potential. *Brain Topography*, *29*(1), 82-93.
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- II. Nowparast Rostami, H., Saville, C.W.N., Klein, C., Ouyang, G., Sommer, W., Zhou, C., & Hildebrandt, A. (submitted). COMT genotype is differentially associated with single trial variability of ERPs as a function of memory type. *Biological Psychology*
- III. Nowparast Rostami, H., Sommer, W., Zhou, C., Wilhelm, O., & Hildebrandt, A. (submitted). Contributions of structural encoding and its top-down modulation to individual differences in face and object cognition: Evidence from the N1/N170 components of the event-related brain potentials. *Cortex*

