Influence of interpersonal abilities on social decisions and their physiological correlates

Dissertation

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Abstract

The concept of interpersonal abilities refers to performance measures using social stimuli which quantify individual differences in social competences and skills that are at the core of interpersonal communication such as the abilities to perceive and remember faces and the abilities to recognize and express emotions. The aim of this dissertation was to examine the influence of interpersonal abilities on social decisions. A particular focus lay on the quantification of individual differences in brain-behavior relationships associated with processing interpersonally relevant stimuli. Study 1 added to existing evidence on brain-behavior relationships, specifically between psychometric constructs of face cognition and event-related potentials (ERPs) associated with different stages of face processing (encoding, perception, and memory) in a familiarity decision. Our findings confirm a substantial relationship between the N170 latency and the early-repetition effect (ERE) amplitude with three established face cognition ability factors. The shorter the N170 latency and the more pronounced the ERE amplitude, the better is the performance in face perception and memory and the faster is the speed of face cognition. Study 2 found that the ability to recognize fearful faces as well as the general spontaneous expressiveness during social interaction are linked to prosocial choices in several socio-economic games. Sensitivity to the distress of others as well as spontaneous expressiveness seem to foster reciprocal interactions with prosocial others. Study 3 confirmed the model of strong reciprocity in that prosociality drives negative reciprocity in the ultimatum game. Using multilevel structural equation modeling (SEM) in order to estimate brain-behavior relationships of fairness preferences, we found strong reciprocators to show more pronounced relative feedback-negativity (FN) amplitude in response to the faces of bargaining partners. Thus, the results of this dissertation suggest that established individual differences in behavioral measures of interpersonal ability are partly due to individual differences in brain mechanisms.

Zusammenfassung

Das Konzept der interpersonellen Fähigkeiten bezieht sich auf Leistungsaufgaben der sozialen Kognition, welche individuelle Unterschiede in der interpersonellen Kommunikation quantifizieren. Diese Aufgaben messen beispielsweise die Fähigkeiten Gesichter zu erkennen und sich diese zu merken sowie Emotionen zu erkennen und diese auszudrücken. Ziel dieser Dissertation war die Untersuchung des Einflusses von interpersonellen Fähigkeiten auf soziale Entscheidungen. Ein besonderer Fokus lag auf der Quantifizierung von individuellen Unterschieden in „brain-behavior" Beziehungen im Rahmen interpersoneller Fähigkeiten. Studie 1 erweiterte bestehende Evidenz zu brain-behavior Beziehungen zwischen psychometrischen Konstrukten der Gesichterkognition und Ereigniskorrelierten Potentiale (EKPs), welche mit den verschiedenen Stadien der Gesichterverarbeitung (Enkodierung, Wahrnehmung, Gedächtnis) während einer Bekanntheitsentscheidung assoziiert sind. Unsere Ergebnisse bestätigen eine substantielle Beziehung zwischen der N170 Latenz und der Amplitude des frühen Wiederholungseffektes (ERE) mit drei Faktoren der Gesichterkognition. Je kürzer die N170 Latenz und je ausgeprägter die ERE Amplitude, umso genauer und schneller ist die Gesichterkognition. Studie 2 ergab, dass die Fähigkeit ängstliche Gesichter zu erkennen sowie die generelle spontane Expressivität während der sozialen Interaktion mit prosozialen Entscheidungen korreliert. Sensitivität für das Leid anderer sowie emotionale Expressivität scheinen reziproke Interaktionen mit Gleichgesinnten zu fördern. Studie 3 bestätigte das Modell der starken Reziprozität, da Prosozialität die negative Reziprozität im Ultimatum Spiel beeinflusste. Unter der Verwendung von mehrebenen Strukturgleichungsmodellen (SEM) entdeckten wir, dass Menschen mit ausgeprägter Reziprozität eine größere Amplitude der relativen „feedback-negativity" (FN) auf das Gesicht von Spielpartnern zeigen. Insgesamt sprechen die Ergebnisse dafür, dass die etablierten individuellen Unterschiede in den Verhaltensmaßen der interpersonellen Fähigkeiten zum Teil auf individuelle Unterschiede in den zu Grunde liegenden neuronalen Mechanismen zurückzuführen sind.

Synopsis

1 Introduction

An aim of contemporary cognitive neuroscience is to translate behavioral evidence into neurological data in order to explain human behavior in terms of its biological underpinnings and to establish so called “brain-behavior relationships”. Cognitive, social, clinical, affective, developmental, and economic neurosciences have produced great progress in the understanding of brain structure and its influence on human cognition. This is not only yielding a new comprehension of human behavior but also offering a new perspective on the reduction problem which arises when simply relating classes of data with different properties to each other. The very common practice in cognitive neuroscience for establishing brain-behavior relationships is the calculation of simple measures of association. This approach does not consider the question how to best model the relationship between mental states in terms of psychological attributes and neurological processes in terms of measured neural activity. However, in order to provide a better understanding of brain-behavior relationships a theoretical conception about the nature of this relationship is indispensable.

Philosophical stances on this relationship – identity vs. supervenience theory – can be translated into psychometric models which provide an empirically testable and sound mathematical foundation for the reduction problem (Kievit, Romeijn, et al., 2011). In identity theory the psychological attributes are identical to and therefore grounded in their physical realization, whereas in supervenience theory the higher order psychological attributes are realized in their neurological properties – they supervene on them. Kievit, van Rooijen, et al. (2011) provide a proof of principle for the supervenience by modelling the brain-behavior relationships of general intelligence (g) using so called Multiple Indicators, Multiple Causes models (MIMIC). Their analyses suggest that contributions from different brain mechanisms to unidimensional g provide the best fit against the data, suggesting a heterogeneous set of physical properties that determine the psychological attribute of general intelligence.

1.1 Aims and outline of the present work

The aim of this dissertation was to apply the exemplified modelling of brain-behavior relationships to the level of social cognition, more specifically by investigating interpersonal abilities and their influence on social decisions. The concept of interpersonal abilities refers to performance measures of social cognition which quantify individual differences in social competencies that are at the core of interpersonal communication. To exemplify, such competencies – characterized as individual differences variables that lie between stable, genetically determined dispositions and easily acquired skills – are for instance the abilities to perceive and remember faces (face cognition) and the abilities to recognize and express emotions. Section 1.2 will provide a more detailed explanation of the concept of interpersonal abilities.

The structure of interpersonal abilities has been investigated in a similar vein as the structure of human intelligence in terms of components of cognitive architecture(Carroll, 1993; Kyllonen, 2002). For instance, Wilhelm et al. (2010) established face cognition as a specific social ability that is clearly distinct from general cognitive ability and object cognition. They identified three component abilities of face cognition – accuracy of face perception, accuracy of face memory, and the speed of face cognition – which showed specific associations with neural indicators of face cognition as measured in event-related-potentials (ERPs) in EEG (Herzmann, Kunina, Sommer, & Wilhelm, 2010).

Study 1 included in this dissertation is a replication and extension of the investigation of brain-behavior relationships in the domain of face cognition. This study helped me to get acquainted with the statistical tools, such as latent difference score modelling (LDS), to associate ERPs from an experimental EEG paradigm to interpersonal ability measures acquired in an independent session. The focus of study 2 was the decoding of emotion expressions from faces and their association with social decisions in terms of prosocial behavior. The analyses have been guided by the empathy-altruism hypothesis (Batson et al., 1991). In this study, I examined the relation of perceptual as well as of expressive emotional abilities to altruism in terms of prosocial behavior. Prosocial behavior was measured with a series of socio-economic games involving a trade-off between self- and other-regarding interests (see section 1.3). The experience I gained by conducting this study and the multivariate modelling of socio-economic choices prepared me for study 3 in which I investigated brain-behavior relationships of fairness preferences in the ultimatum game in terms of individual differences in reciprocity.

A common denominator of the three studies is the establishment of links between interpersonally relevant traits and individual differences in measures of physiological activity. Following the person-situation debate between 1970 and 1990 (Mischel, 1990) the biopsychological personality research distinguishes two perspectives onto the interaction of personality trait and situational influences in determining individual differences in behavior and physiological processes. A personistic perspective on trait-physiology assumes habitual, transsituationally stable individual differences in physiological responses, whereas an interactionistic conceptualization supposes that traits as dispositions are only active in certain situational contexts. Evidence favors the interactionistic account in that situational context and its subjective representation by the participants moderate the trait–physiology relationships for both peripheral and central nervous system activity (Stemmler & Wacker, 2010). Hence, the study design should allow measuring both, stable individual differences in interpersonal ability tasks, as well as situationally-bound physiological reactions evoked by a specific manipulation of the situational context. In most analyses of the presented studies we did not quantify individual differences in ERPs per se, but individual difference in relative ERP parameters, measured as difference waves between experimental conditions. In study 1 we were for example interested in the neurophysiological correlates of face memory. We hypothesized that the early and late repetition effects (ERE and LRE) reflecting the re-activation of both stored facial structures (ERE) and person-identity information (LRE) should account for variance in a latent variable representing face memory ability. In order to evoke ERE and LRE, a specific experimental manipulation is required, namely the comparison of ERPs in response to primed and unprimed face stimuli. This exemplifies how the priming manipulation reflects a changing situational variable which allows us to quantify the neurophysiological correlates of face memory, namely the ERE and LRE, that are parameterized by calculating the difference amplitude waves between primed and unprimed face processing. Similarly, in study 3 we contrasted the ERPs elicited by faces of unfair compared to fair bargaining partners and used this difference wave, the feedback-negativity (FN) as a neural indicator of fairness preferences. Section 1.4 will focus on the applied statistical tools to use difference waves such as ERE or FN in the modelling of brain-behavior relationships.

1.2 Interpersonal abilities

The face is a mirror reflecting crucial information about the person we are interacting with. Not only does it reveal age, gender, ethnicity and attractiveness but it also serves as a medium to transmit social signals, like emotions. Functional and neuroanatomical models of face cognition (Bruce & Young, 1986; Calder & Young, 2005; Haxby, Hoffman, & Gobbini, 2002) assume two relatively independent processing streams for the recognition of identity and the recognition of facial expressions such as manifestations of emotions. Recognizing the identity of a face consists of perception, encoding and re-activation of invariant facial features in the lateral fusiform gyrus (Gobbini & Haxby, 2007; Haxby et al., 2002). Recognizing emotion from facial expressions requires a distributed neural system that consists of multiple, bilateral regions. Early perceptual processing of faces happens in occipital and temporal lobes which construct detailed representations from the configuration of facial features (core system). Subsequent recognition of emotion draws on a set of brain structures, including amygdala, anterior insula and orbitofrontal cortex, which relates perceptual representations of the face to the generation of knowledge about emotion and social cues (extended system) (Adolphs, 2002a, 2002b; Haxby et al., 2002). The processing stages postulated in neurocognitive models of person recognition suggests that a separation between perceptual and mnemonic processes should be applied when studying individual differences in behavioral interpersonal ability tasks of face (Wilhelm et al., 2010) and emotion recognition (Hildebrandt, Sommer, Schacht, & Wilhelm, 2015).

Emotion recognition accuracy (ERA) from faces has been conceptualized as a performance measure of emotional intelligence, next to higher order ability branches, such as assessing, understanding, and managing one’s own and also other people’s emotions (Mayer, Salovey, Caruso, & Sitarenios, 2001). ERA is associated with, but separable from, general cognitive ability factors (e.g. Mayer, Roberts, & Barsade, 2008) and is related to better social adjustment and mental health (Carton, Kessler, & Pape, 1999; Izard et al., 2001; Montagne et al., 2005; Nowicki & Duke, 1994). Previous research points to a link between ERA and prosocial behavior. Hence, on the one hand, ERA promotes the effectiveness of economic negotiations, both in terms of creating value (joint outcome) and a greater share for oneself (Elfenbein, Foo, White, Tan, & Aik, 2007). On the other hand, ERA is negatively correlated with self-interested manipulative behaviors such as Machiavellianism (Wai & Tiliopoulos, 2012).

Guided by the empathy-altruism hypothesis, that states prosocial motivation evoked by empathy to be directed toward increasing the welfare of a person in need (Batson et al., 1991; Batson & Moran, 1999), in study 2 we hypothesized that ERA will be associated with prosocial behavior in socio-economic games. Empathy is a broad concept, disputed both in its nature and prevalence across species and age groups. The Perception-Action-Model (PAM) provides a useful theoretical account for empirical findings about different levels of empathy, such as emotional contagion, sympathy, empathy, cognitive empathy, or prosocial behavior. According to PAM, empathy requires the perception of emotional facial expressions (Preston & de Waal, 2002). Indeed, highly empathic persons show stronger facial reactions to facial expressions of others and this tendency is accompanied by higher empathic accuracy (Dimberg, Andréasson, & Thunberg, 2011). Using structural equation modelling, Kunecke, Hildebrandt, Recio, Sommer, and Wilhelm (2014) reported a substantial relationship between emotion-related facial reactions, measured with the electromyogram, to dynamic emotional facial expressions and emotion perception ability, providing evidence for the role of facial muscle activation in emotion perception from an individual differences perspective. Therefore, the ability to recognize emotions in others but also the tendency to express emotions oneself seem to be core components of empathy and may influence decisions on social cooperation.

In study 2 we considered an ability perspective onto empathy as promising since most research on the relationship between empathy and prosocial behavior has induced empathic states (Batson & Ahmad, 2001; Batson & Moran, 1999; Leiberg, Klimecki, & Singer, 2011; Rumble, Van Lange, & Parks, 2010), or relied on self-reports of trait empathy (Edele, Dziobek, & Keller, 2013; Pavey, Greitemeyer, & Sparks, 2012). Both approaches may be compromised by effects of social desirability (Lucas & Baird, 2006). This assumption is supported by the comprehensive literature on distortions of self-reported personality traits (see Ziegler, MacCann, & Roberts, 2011) and of measures of trait emotional intelligence (e.g. Kluemper, 2008), including empathy (e.g. Kämpfe, Penzhorn, Schikora, Dünzl, & Schneidenbach, 2009). The perspective on empathy as being an ability that can be measured by capturing performance is more robust against social bias, but it attracted less research attention. In this dissertation however ERA has been considered an ability proxy of empathy.

Interestingly, apart from emotion recognition also emotion expression may be associated with prosocial behavior. Inspired by the assumption in evolution theory that cooperation among non-kin may evolve in a population through the identification of honest and non-falsifiable signals (Dawkins, 1976; Hamilton, 1964), it is argued that nonverbal signals such as spontaneous or voluntary emotional expressivity can act as a marker for cooperative behavior or trustworthiness (DeSteno et al., 2012; Frank, 1988; Scharlemann, Eckel, Kacelnik, & Wilson, 2001). Expressivity may help to identify cooperative individuals since cooperators display more positive emotions such as Duchenne (spontaneous) smiles compared to non-cooperators (Brown, Palameta, & Moore, 2003; Mehu, Grammer, & Dunbar, 2007). Schug, Matsumoto, Horita, Yamagishi, and Bonnet (2010) examined the spontaneous expression of emotions in game partners when faced with unfair behavior. Cooperators, defined by their propositions in the ultimatum game, displayed greater amounts of positive as well as negative spontaneous emotional expressions when responding to unfair offers, suggesting that cooperators may be generally more expressive than non-cooperators. The authors speculate that general emotional expressivity might be a more dependable signal of cooperative tendency than the display of positive emotion alone. In line with the interactionist account of biopsychological personality research (Stemmler & Wacker, 2010) that conceptualizes traits as dispositions that are only active in certain situational contexts we assessed the trait of emotional expressivity in a well-defined and experimentally manipulated interval of the Prisoner’s Dilemma (see section 1.3). This interval was the time window in which the participant received feedback about the co-player’s decision to cooperate or defect. This allowed us to study spontaneous emotional expressions in a situational context, where participants were exposed to meaningful stimuli and therefore motivated to show specific emotional reactions when learning about whether their co-player decided to cooperate or defect. We tried to construct an ecologically valid and reciprocal interaction situation by displaying each co-player's face on screen and informing the participants that their co-players would also see their own picture.

1.3 Socio-economic games

Socio-economic games are social decision-making tasks simulating real-world strategic interactions (Camerer, 2003). The games that have been used in this dissertation involve two individuals within one decision-making period who make monetary choices based on an interdependent pay-off matrix. The two bargaining partners are given a set of rules and they face limited information since they are confronted with uncertainty about the other's intentions. Importantly, the individuals' choices alter not only their own outcome, but also the outcome of the other, allowing the researcher to study prosocial behavior, defined as tendency to enhance both joint outcomes and equality in outcomes (Van Lange, 1999). In its original mathematical formulation game theory hold the normative assumption of economic rationality (Von Neumann & Morgenstern, 1944), which claims that individuals maximize their personal gain. However, later experiments in behavioral economics (Fehr & Fischbacher, 2002; Fehr, Fischbacher, & Gächter, 2002; Fehr & Schmidt, 1999) exposed that human behavior deviates from conventional economic assumptions of self-interest and rationality (homo oeconomicus), in that many people have a tendency to intentionally cooperate.

One of the most extensively studied socio-economic games to measure cooperation behavior is the Prisoner's Dilemma (PD). Here participants can cooperate or defect with a second player, such that individual earnings are maximized by defection but collective earnings are maximized by cooperation. According to Nash (1950) the rational choice is to defect since this maximizes individual earnings (Nash equilibrium). Nevertheless, in one-shot PD games, where partners are encountered only once, people tend to cooperate with a rate of 42 % (Sally, 1995), displaying altruistic, cooperative behavior (Lee, 2008). Accounts of cooperative behavior in PD assume stable individual differences (Brosig, 2002). For example, Kuhlman and Marshello (1975) observed that some participants always prefer to cooperate with their partners while others either defect or use a mixed strategy such as tit-for-tat. In an iterated PD tit-for-tat means that one player will first cooperate and then subsequently replicate an opponent's previous action. This is one form of reciprocity describing the reward of kind actions (positive reciprocity) and the punishment of unkind actions (negative reciprocity) (A. Falk & Fischbacher, 2006; Fehr & Simon, 2000).

Negative reciprocity can be measured in the ultimatum game (UG), which is a two-stage game where two individuals, a proposer and a responder, bargain over a fixed amount of money. First, the proposer offers a split of his endowment, and subsequently, the responder decides to accept or reject the offer. If accepted, each bargainer receives money according to the offer; if rejected, each bargainer receives nothing. According to economic rationality the responder should accept any offer to maximize personal gain. However, responders tend to show negative reciprocity by rejecting very unfair offers (Güth, Schmittberger, & Schwarze, 1982). Previous research suggests that there are individual differences in negative reciprocity since only 50% of the responders reject unfair offers in which they receive less than 30% of the total sum (Camerer, 2003).

Since research has revealed substantial individual differences in social preferences in socio-economic games, the aim of the dissertation (study 2 and 3) was to shed some light on the psychophysiological factors that may determine individual differences in social decisions, such as cooperation. As already pointed out in section 1.2, empathy theories suggest that interpersonal abilities such as emotion recognition and emotion expression foster cooperation (study 2). A second research question that we were interested in concerned the role of personality in fairness preferences such as negative reciprocity (study 3), since previous research theorizes that interpersonal traits are at the source of the behavioral heterogeneity in socio-economic games (for a comprehensive review seeZhao & Smillie, 2015).

1.4 Methods to establish brain-behavior relationships

ERPs are not only a useful method to understand and evaluate cognitive, affective, motor and sensory processes within one individual, but they can also provide biomarkers for individual differences in interpersonal traits. For instance, Smillie, Cooper, and Pickering (2010) examined the influence of extraversion, a trait hypothesized to be originated from individual differences in the dopamine system, and a dopamine-related gene polymorphism, on FN during an associative reward-learning paradigm. Unpredicted non-reward evoked the most negative FN while unpredicted reward led to the least-negative FN. A difference wave comparing these conditions was significantly more pronounced for extraverts than for introverts. While the gene polymorphism did not significantly modulate the FN, it was significantly associated with extraversion. The calculation of difference waves between the ERPs elicited by two contrasted experimental conditions is a common tool in cognitive neuroscience (Luck, 2005). The difference wave reveals the time course and scalp distribution of the underlying component, arising from synchronized synaptic activity in populations of cortical neurons (Kandel, Schwartz, & Jessell, 2000), that differs across conditions.

Study 1 and 3 of this dissertation used such difference waves as biomarkers for individual differences in interpersonal traits. In contrast to Smillie et al. (2010), we did not analyze group differences (i.e. extraverts vs. introverts) in average difference waves, but were interested in studying the continuous relationship between neural indicators and interpersonal abilities (study 1) or traits (study 3). We therefore used structural equation modeling (SEMs) to estimate the relationships between latent factors consisting of multiple continuous indicators of ERP parameters and interpersonal ability/trait scores.

Latent factors represent the common variance of multiple indicators on a measurement-error-free level (Bollen, 1989). Indicators that assess the same latent factor should correlate more highly with one another than with indicators that assess different latent factors. The problem with using difference waves in SEM is that they are inherently unreliable (McArdle & Nesselroade, 1994; Nesselroade, Stigler, & Baltes, 1980) and therefore often prevent the convergence of a latent factor of difference scores. Here, the latent difference score technique (LDS; McArdle, 1988) has been particularly valuable in modeling small amplitude differences between two experimental conditions. LDS therefore allows for circumventing the reliability concerns often associated with any kind of difference scores. LDS parameterizes the difference between two ERPs on a latent level by controlling for measurement error. Such differences between ERPs are implicit in components like ERE and LRE, which are defined as the amplitude deviation between the processing of primed and unprimed faces. Similarly, the FN is defined as the amplitude difference between a bad and a good outcome in a bargaining context.

For simplicity, the LDS is here described with the example of ERE as it was applied in study 1. We considered the priming conditions as the targeted experimental condition (see section 2.1). We assumed that the latent variable representing individual differences in priming effects could be explained by the baseline condition (unprimed) and the difference between the baseline and the targeted condition. The regression of the primed condition onto the unprimed condition and the regression of the primed condition onto the difference value (ERE) are modeled as a "perfect regression" (fixed to 1), since the primed condition is assumed to be completely determined by the baseline value and the difference between baseline and the experimental condition. This variance decomposition allowed for modeling the latent difference between primed and unprimed conditions, and therefore provided a measure of the ERE on a latent level. The latent difference variable represented individual differences in the neural signal of re-activating stored facial features that could be set in relation to face cognition ability scores.

2 Summary of the present studies

2.1 "Neurocognitive mechanisms of individual differences in face cognition: A replication and extension" (study 1, Kaltwasser et al., 2014)

Bruce and Young (1986) proposed a functional model to describe the serial recognition process of familiar faces. The output of an initial structural encoding (step 1) is matched with previously stored structural codes (face recognition units – step 2) before identity-specific semantic codes are accessed from person identity nodes (step 3), and finally names are retrieved. Previous work confirmed the involvement of specific ERPs in each processing step of this functional model. As a first step for instance the N170, characterized by a negative peak at occipito-temporal sites around 150-190 ms, which is larger for faces than for other objects, is considered to reflect configural encoding of facial features and their integration into a holistic percept (Eimer, 2011). In step 2, the ERE is associated with the activation of structural representations of faces in long-term memory and with the identification of familiar faces (Schweinberger & Burton, 2011). Being operationalized as the difference wave between ERPs to primed and unprimed faces in priming tasks and most pronounced at temporo-parietal sites around 260-330 ms, the ERE is larger for familiar as compared to unfamiliar faces (Schweinberger, Pfütze, & Sommer, 1995; Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002). The psychometric work on individual differences in face cognition (Hildebrandt, Sommer, Herzmann, & Wilhelm, 2010; Hildebrandt, Wilhelm, Schmiedek, Herzmann, & Sommer, 2011; Wilhelm et al., 2010) is in line with the model of Bruce and Young (1986) in that there is a clear separation between processes of face perception and face memory. The follow-up study on brain-behavior relationships of face cognition (Herzmann et al., 2010) measured ERP components in a face priming paradigm and, in independent tasks and sessions, assessed face cognition abilities using the same psychometric task battery of face cognition abilities. A limitation of this study by Herzmann and her colleagues (2010) was that individual differences in the accuracy of face perception and face memory were empirically undifferentiated. This might have been the case because the behavioral testing had been completed after the ERP experiment, leading to a dedifferentiation of these abilities due to training. The main aim of study 1 of this dissertation was to perform a replication of Herzmann et al. (2010) with a reversed experimental sequence of behavioral testing and physiological recording, in order to capture distinguishable face perception and face memory accuracy factors. We assessed the robustness of the findings with a slightly modified experimental task and a larger sample size. In order to replicate and extend these findings, we tested 110 participants on a comprehensive task battery measuring face cognition and general cognitive abilities, as represented in the structure of intelligence, followed by ERP recordings in a face learning and recognition task. This recognition task consisted of a familiarity decision on target faces that were previously learned, along with a set of faces that were unfamiliar to the participant. The target faces were either primed by the presentation of the same face identity 1800 ms before target onset ("primed") or by the presentation of an unfamiliar face ("unprimed").

We replicated the link between ERP components indicating the speed of structural face encoding (N170 latency) and access to structural representations in memory (ERE) to the accuracy and speed of face cognition and to established cognitive abilities. Importantly, we extended the findings of Herzmann et al. (2010) in showing that not only face cognition accuracy per se is predicted by those ERPs, but that this relationship persists if we distinguish between face perception and face memory. The shorter the N170 latency, that is, the faster a person creates structural representations of faces, the better is her or his performance in face perception and memory and the faster is the speed of face cognition. Since the functional significance of the N170 may encompass not only structural encoding, but further configural and holistic encoding (Deffke et al., 2007; Eimer, 2011), it is plausible that interpersonal variations in face cognition abilities are related with these basic processes. Hence, fast configural and holistic processing of faces seems to be a foundation for accurately learning and recognizing faces.

Furthermore, individuals with more pronounced ERE amplitudes for familiar faces were faster and more accurate in face perception and memory, which in turn, has been associated with a more efficient activation of representations of faces, presumably localized in fusiform face-responsive regions (Eger, Schweinberger, Dolan, & Henson, 2005; Schweinberger et al., 2002). A novelty of the present study was the use of an unfamiliar face mask after each prime. The mask was introduced by Doerr, Herzmann, and Sommer (2011) with the purpose of eliminating contributions of perceptual codes to face priming. Since the brain-behavior relationships for the ERE remained largely unaltered by using a mask, we can conclude that the contribution of the access to structural face codes of known people in memory to individual differences in face cognition is not significantly confounded with priming effects of perceptual codes in vision.

We extended findings of Herzmann et al. (2010) by using nested structural equation models with established cognitive abilities such as working memory, reasoning, immediate and delayed memory, mental speed and object recognition speed. This technique enabled us to control for face perception-related variance in face memory tasks by nesting face memory under face perception. This allowed us to test the distinction between face perception and face memory observed at the performance level, also at the neurocognitive level. We predicted that face perception and face memory can be separated statistically in the measurement model of face cognition abilities, and that they also show differential relationships with ERPs. Indeed the results suggest that the N170 latency reflects a face-specific perceptual-speed factor, whereas the ERE seems to be a non-face-specific, general speed indicator. Our results further indicate that the P100 amplitude is involved in face-specific memory related processes. This finding was unexpected and is at variance with our previous results. However, it could be explained with a mechanism of selective attention as a study by Rutman, Clapp, Chadick, and Gazzaley (2010) suggests: To investigate the influence of selective attention on working memory (WM) recognition, they studied the temporal dynamics of top-down modulation in a selective, delayed-recognition paradigm. Participants saw overlapped, “double-exposed” images of faces and natural scenes. They were instructed to either memorize the face or the scene while simultaneously ignoring the other stimulus. Rutman et al. (2010) could show that the degree to which participants modulate the early P100 during selective stimulus encoding significantly correlated with their subsequent WM recognition.

In conclusion, study 1 replicated and extended several previously established brain-behavior relationships (Herzmann et al., 2010) between psychometric constructs of face cognition and ERP components associated with different stages of face processing (encoding, perception, and memory). Applying multivariate behavior measures and a modified repetition priming paradigm in independent sessions with new stimulus material we were able to distinguish between the accuracy of face perception and face memory as well the speed of face cognition in the measurement model, which had not been possible in the previous study. Our findings revealed a substantial relationship between the N170 latency and the ERE amplitude with all three face cognition abilities, indicating that persons with faster structural encoding of faces are also quicker to activate brain regions necessary to encode faces configurally and holistically such as lateral fusiform gyrus (Gobbini & Haxby, 2007; Haxby et al., 2002).

2.2 “On the relationship of emotional abilities and prosocial behavior” (study 2, Kaltwasser et al., submitted)

By assessing individual differences in ERA and spontaneous emotion expressions during social interaction, study 2 examined how the different subcomponents of empathy according to PAM (see section 1.2) are related to prosocial behavior in socio-economic games. Our main question was whether there is an overall domain-general relationship between emotional abilities and prosocial behavior, or whether there are differential relationships for specific emotion categories. The conception of innate and instantly recognizable specific emotions, initially formulated by (Darwin, 2002/1872), was supported by Ekman and Friesen (1971) who described six primary emotions: Anger, disgust, happiness, fear, sadness and surprise. These primary emotions were found to be consistent in their expression across cultures and in other primates. Basic emotion theories imply that different emotions serve specialized interpersonal functions and consider emotions as coordinated systems of response shaped by natural selection because they increase fitness in specific situations (Nesse, 1990). The use of specific social signals may be explained in terms of adaptive functions advanced through evolution. For instance, social species, like primates, use nonverbal expressions of subordination or fear to avoid becoming targets of aggression by dominant conspecifics (Preuschoft, 1999).

In humans, the ability to recognize emotion expressions of distress such as fear and sadness seems to be linked to prosocial behavior (Marsh & Ambady, 2007; Marsh & Blair, 2008; Marsh, Kozak, & Ambady, 2007). Participants who more accurately recognized fear in a standard facial expression recognition task, also donated more to victims in a classic altruistic paradigm, acted more favorably in an alleged attractiveness rating task of other participants or reported more sympathy and desire to help. Furthermore, a meta-analysis by Marsh and Blair (2008) confirmed a link between antisocial behavior and specific deficits in recognizing fearful and sad expressions. The relationship between prosocial behavior and fear recognition can be explained by a concern mechanism (Nichols, 2001) or violence inhibition theory (Blair, 1995); according to these theories the correct interpretation of another's distress cues induces empathic processes that increase the likelihood of prosocial behavior and decrease the likelihood of antisocial behavior. As described in section 1.2, study 2 furthermore aimed at testing the theory according to which nonverbal signals such as emotional expressivity can act as a marker of cooperative behavior (Frank, 1988; Scharlemann et al., 2001).

In order to test the relationship of receptive and spontaneous expressive emotional abilities with prosocial behavior we applied a multivariate approach with a focus on individual differences. Participants played three socio-economic games widely used in behavioral economics and undertook three standardized tests of ERA for six emotion expressions: Anger, disgust, fear, happiness, sadness, and surprise. We also recorded spontaneous emotion expressions in response to feedback about the co-player's cooperation or defection in PD. Furthermore, participants completed a questionnaire of social value orientation (SVO; Murphy, Ackermann, & Handgraaf, 2011). The concept SVO extends the rational self-interest postulated in economic theory by assuming that individuals also tend to pursue broader goals such as equality in outcomes. The magnitude of concern people have for others can be measured by a 6-item questionnaire about how participants would share resources with an anonymous stranger (Murphy et al., 2011).

By using several independent indicators, we modeled the relationship between the constructs of ERA and prosocial behavior at the level of latent factors – abstracting from measurement error and task specificity. Importantly, we tested the association of each basic emotion recognition performance to prosocial behavior, which allowed us to determine differential social signaling functions of different emotion categories. In contrast to most of the research regarding the influence of empathy or ERA on prosocial orientation, we measured prosociality in terms of cooperative choices, alas actual behavior. We consider it important to know whether the expected association between emotional ability and prosociality generalizes beyond lab procedures of helping behavior (e.g., donation) to standard measures of social preferences.

We expected overall ERA to predict prosocial behavior. Regarding the signaling function of specific emotion categories, we hypothesized prosocial behavior to be most strongly associated with the ability to recognize distress-related emotions such as fear. Furthermore, we predicted that cooperators display more spontaneous expressions than non-cooperators during feedback about the co-player's response.

While there was no meaningful overall relationship of ERA with cooperative behavior in the socio-economic games, emotion specific analyses revealed that particularly the ability to recognize fearful and sad faces was associated with prosocial behavior and social value orientation. Also, the tendencies towards showing more smiles after learning about cooperation as well as showing more anger, less surprise, and fewer neutral expressions after learning about defection during the PD were linked to prosocial behavior. This is in line with a face-to-face study with a one-shot PD investigating whether cooperative individuals can credibly signal their intentions and whether this can be recognized by interaction partners (Brosig, 2002). Results revealed that both abilities, signaling and recognizing, are related to the individual's tendency to cooperate.

Our findings of an emotion-specific link between ERA and prosocial behavior as measured with standard socio-economic games, as well as with SVO, replicate previous research showing that the ability of recognizing fearful faces is related to prosocial behavior (Marsh & Ambady, 2007; Marsh & Blair, 2008; Marsh et al., 2007). This is in line with theories postulating a concern mechanism (Nichols, 2001), as well as with the empathy-altruism hypothesis (Batson et al., 1991). Both theories assume that the sensitivity to the emotional state of a person in distress or need triggers the motivation to help.

Regarding emotion expression our results support studies using human coders of emotion expression that found cooperative and altruistic individuals to display higher levels of positive emotion than non-cooperators (Brown et al., 2003; Mehu et al., 2007), and to be generally more expressive when faced with uncooperative behavior (Schug et al., 2010). Emotion theories suggest that anger signals aggressiveness and rejection (Frijda, Kuipers, & Terschure, 1989; Plutchik, 1997) and triggers trait inferences of high dominance and low affiliation (Hess, Blairy, & Kleck, 2000; Knutson, 1996). Moreover, an expectation of competition instead of cooperation promotes the expression of anger (Lanzetta & Englis, 1989). It is therefore conceivable that prosocial individuals are motivated to express more anger in response to defection in order to support cooperative behavior: The tendency to express more negative emotion when confronted with defection but more positive emotion when faced with cooperation provides prosocial individuals with opportunities to choose other cooperative individuals as interaction partners. In all, cooperative individuals seem to be more sensitive to the distress of others and more expressive, possibly fostering reciprocal interactions with like-minded others.

2.3 "Behavioral and neuronal determinants of negative reciprocity in the ultimatum game" (study 3, Kaltwasser et al., submitted)

While study 2 dealt with individual difference in active cooperation behavior in terms of prosocial choices, study 3 investigated why persons differ in reactive cooperation in terms of their responder behavior in the UG (see section 1.3). A responder shows negative reciprocity by rejecting unfair offers. The model of strong reciprocity claims that negative reciprocity reflects prosociality since the rejecting individual is sacrificing resources in order to punish unfair behavior (Fehr et al., 2002). However, Yamagishi et al. (2012) provided evidence against the strong reciprocity account since they did not find any correlation between negative reciprocity and prosocial behavior in other games. Instead, they found the rejection rate of unfair offers to be linked to the personality trait of assertiveness. They proposed that assertive participants use a tacit strategy to avoid the imposition of an inferior status. Clearly, people differ in negative reciprocity – but which motivation drives this variance in behavior?

Osinsky, Mussel, Ohrlein, and Hewig (2014) studied neuronal processes of social evaluation by recording the EEG while participants played the UG. The participants repeatedly received fair or unfair monetary offers from alleged other participants shown as portraits with neutral facial expressions. The faces could be used as predictive cues for the fairness of offers since some proposers would always make fair offers while others would only make unfair offers. Osinsky et al. (2014) measured the FN in response to the portraits of the different proposers and to their offers. The FN is an event-related-potential (ERP) characterized by a frontocentral negativity 300-500 ms after an unfavorable relatively to a favorable event (Miltner, Braun, & Coles, 1997). It has been explained as an indicator of 'good-vs-bad evaluation' (Hajcak, Moser, Holroyd, & Simons, 2006), stemming from the dopaminergic signaling of reward prediction errors forwarded to medial frontal cortex (Gehring & Willoughby, 2002; Holroyd & Coles, 2002). Interestingly, in the study by Osinsky et al. (2014) not only unfair relative to fair offers triggered a FN as in previous studies using the UG (Boksem & De Cremer, 2009; Hewig et al., 2011; Van der Veen & Sahibdin, 2011; Wu, Zhou, van Dijk, Leliveld, & Zhou, 2011), but also – over the course of the experiment – the faces of unfair compared to fair bargaining partners. This result corroborates previous research with fMRI where an affective value was associated with an opponent in repetitive interpersonal bargaining, based on her/his fairness in the preceding interaction history (Singer, Kiebel, Winston, Dolan, & Frith, 2004; Singer et al., 2006). Thus, Osinsky et al. (2014) discovered a basic neural mechanism of social evaluation during the UG, which was sensitive not only to the valence of monetary offers but also to learned fairness features of the proposers. This latter mechanism of social evaluation might also be indicative for individual differences in fairness preferences of the responders, that is, the evaluation of the proposers fairness may depend on the fairness preferences of the responder.

In study 3, we aimed to investigate individual differences and neuronal correlates of negative reciprocity in the UG. Specifically, we were interested in understanding the motivation which promotes the rejection of unfair offers. We modelled brain-behavior relationships in negative reciprocity by applying a multilevel and multivariate approach with measures of personality and fairness preferences. We used the same measure of prosocial behavior (SVO; Murphy et al., 2011) and a similar measure of assertiveness that were applied in Yamagishi et al. (2012). We hypothesized that both, prosociality and assertiveness are linked to the rejection of unfair offers in UG. Following up on the work by Osinsky et al. (2014), we expected the FN to indicate the fairness of both offers and proposers (faces). Moreover, we expected that negative reciprocity should drive the effects of individual differences in FN in response to the fairness of the proposer. Our rationale was that participants with stronger fairness concerns in terms of negative reciprocity should show more pronounced fairness effects in FN in response to the proposer's face.

Using SEM with a sufficiently large sample of $N = 200$, we found that both prosociality as well as assertiveness significantly predicted negative reciprocity measured by the rejection rate of unfair offers in UG. Furthermore, the results confirmed the FN as an indicator of social evaluation, since the faces of unfair and fair proposers elicited a significantly more negative amplitude 220-352 ms after face onset characterized by a frontocentral negativity. A second step of analysis linked the experimental within-subject effects of fairness of the proposer in FN amplitude to the measurement model of individual differences in negative reciprocity. Here we used multilevel SEM (mSEM) to investigate brain-behavior relationships of fairness preferences. The results revealed that the FN amplitude evoked by unfair and fair proposers relative to neutral ones was most pronounced in participants exhibiting stronger negative reciprocity in terms of rejection rates of unfair offers in UG. The mSEM did not provide evidence that assertiveness or prosociality significantly predicts relative FN amplitude.

Our results suggest several motivations driving negative reciprocity. On the one hand, our positive finding of prosociality predicting negative reciprocity supports the theory that prosocial participants follow strong reciprocity by sacrificing their own resources in order to punish unfair behavior (Axelrod & Hamilton, 1981; Fehr et al., 2002; Fehr & Gächter, 2002).

On the other hand, our finding that also assertiveness has a significant influence on negative reciprocity suggests that emotional styles or personality traits lead people to punish unfair behavior, allowing them to preserve integrity and avoid the imposition of an inferior status (Yamagishi et al., 2012).

In ERPs we did not find a significant difference in the neural response elicited by the face of unfair and fair proposers, but between both unfair and fair as compared with neutral proposers. This suggests differential neural mechanisms being involved in the processing of faces associated with different fairness conditions as compared with provided offers in our study. The FN found here in response to a proposer's face seems to be an emotion signal coding a general social arousal effect which might be similar to the processing of emotional context information in faces (Abdel Rahman, 2011; Wieser & Brosch, 2012). Our brain-behavior analysis with mSEM suggests that this social arousal effect is particularly evolved in strong reciprocators corroborating the results by Boksem and De Cremer (2009) where people with higher fairness concerns in terms of moral identity showed a more pronounced relative FN in response to offers in the UG. In our study this effect was transferred to the face of the proposer, suggesting that the FN is truly a social signal reflecting social evaluation and processing of personal reputation.

3 General discussion and future directions

The present dissertation researched the neurobiological basis of individual differences in interpersonal abilities and traits and their relations with social decisions. Study 1 extended existing evidence on brain-behavior relationships (Herzmann et al., 2010) between psychometric constructs of face cognition and ERP components associated with different stages of face processing (encoding, perception, and memory). Our findings confirm a substantial relationship between the N170 latency and the ERE amplitude with all three face cognition abilities. The shorter the N170 latency and the more pronounced the ERE amplitude, the better is the performance in face perception and memory and the faster is the speed of face cognition. Study 2 found that the ability to recognize fearful faces as well as the general spontaneous expressiveness during social interaction are linked to prosocial choices in several socio-economic games. Sensitivity to the distress of others as well as spontaneous expressiveness seem to foster reciprocal interactions with prosocial others. Study 3 confirmed the model of strong reciprocity in that prosociality drives negative reciprocity in the ultimatum game. Using multilevel SEM in order to model brain-behavior relationships of fairness preferences, we found strong reciprocators to show more pronounced relative FN amplitude in response to the faces of bargaining partners.

In the following I will first discuss the measurement of associations between interpersonal traits and physiological variables (section 3.1). In this section I will focus on methodological challenges when estimating brain-behavior relationships of social cognition which made us apply performance measures of interpersonal abilities in SEM instead of correlating self-report scales with physiological data on a manifest level. Thereafter, I will comment on the use of socio-economic games to quantify individual differences in social interaction (section 3.2) before I turn to a broader discussion about the use of brain-behavior relationships in order to study a representative brain in modern “population neuroscience” (section 3.3). Unresolved questions and suggestions for future research are discussed along the way.

3.1 Brain-behavior relationships of interpersonal abilities

Differential psychology encompasses the psychometric assessment of abilities and personality with special emphasis given to their real-world significance, their developmental antecedents and their social consequences (Lubinski, 2000). With the advancement of neuroscientific tools such as EEG and fMRI more research was devoted to the investigation of the biological basis of individual differences in cognition, such as in intelligence research (Hendrickson & Hendrickson, 1980; Jensen, 1998), but later also in affective and social processes. The first studies (Sternberg, 1997; Tomarken, Davidson, Wheeler, & Doss, 1992) in this latter domain were based on psychophysiological personality theories such as Eysenck's theory asserting that low cortical arousal accompanies extraversion (Eysenck, 1967), and Gray's reinforcement sensitivity theory (for a discussion of the translation of Gray's theory in the animal model to the study of individual differences in humans see Markett, Montag, & Reuter, 2014). Gray's theory claims that impulsivity is associated with high sensitivity to signals of reward, whereas anxiety is accompanied with high sensitivity to signals of punishment (Gray, 1982, 1987). Also, the theory by Davidson (1992), that individual differences in approach- and avoidance-related emotional reactivity and temperament are linked to stable differences in baseline measures of activation asymmetry in anterior regions, forwarded research on brain-behavior relationships of interpersonally relevant traits.

The advance of social neuroscience using fMRI increased the number of studies reporting correlations between measures of individual differences relating to emotion, personality, and social cognition and measures of neural activity. For instance, Singer, Seymour, et al. (2004) report the size of differential activation in anterior cingulate cortex and left insula induced by an empathy-related manipulation to be correlated between .52 and .72 with self-report measures of emotional empathy (Balanced Emotional Empathy Scale of Mehrabian and Empathic Concern Scale of Davis). Studies like this drew a lot of attention in the young field of Neuroeconomics, but they were soon to face scrutinizing reception by the scientific peer community: In an article in *Perspectives on Psychological Science* Vul, Harris, Winkielman, and Pashler (2009) reviewed social neuroscience studies using fMRI and pointed to unusually high (>.8) correlations between brain activation and personality measures. While their argument regarding the inflated brain-behavior correlations due to non-independent analyses ("double dipping") was disputed by scientists whose studies were reviewed (Lieberman, Berkman, & Wager, 2009), Vul et al. (2009) also claimed that the considered brain-behavior correlations are higher than should be expected given the limited reliability of both fMRI and self-report personality measures. Since the correlation coefficient is calculated as the ratio between the covariance of two measures and the product of their standard deviations, the reliabilities of the two measures provide an upper bound on the possible size of the correlation (Nunnally, 1970).

In the studies of the present dissertation we suggest an alternative approach to the investigation of brain-behavior relationships in the interpersonal domain which offers a more reliable, and importantly, more valid account of individual differences in brain-behavior relationships of social cognition. In study 1 and 2 we applied performance-based instead of self-reported measures of interpersonal abilities because only these adequately conceptualize ability constructs (Wilhelm, 2005) and are less likely to be distorted by response biases (Kämpfe et al., 2009; Kluemper, 2008). Moreover, we were not calculating a manifest correlation between one measure for individual differences in an interpersonal trait (such as a self-report empathy scale) and one neuronal parameter (such as relative physiological activation in a specific region). By employing SEM and LDS we rather established brain–behavior relationships on a latent, and therefore measurement-error-free level. Using several indicators per latent interpersonal ability factors we were therefore able to estimate individual differences in interpersonal abilities in a more reliable and valid manner.

However, both in studies 1 and 3 problems arose when modelling brain-behavior relationships of rather late ERPs in the form of difference waves such as the ERE, LRE and FN. While the brain-behavior relationships of earlier components – as the association between N170 latency with accuracy of face perception, face memory and speed of face cognition (Herzmann et al., 2010; Kaltwasser, Hildebrandt, Recio, Wilhelm, & Sommer, 2014) – showed stability across studies, the brain-behavior relationships of the later difference components were more difficult to model. The reason for this challenge was that they often showed limited inter-individual variance, so that modeling their relation to individual differences in behavioral measures was not always possible. Even when we established the difference scores on a latent level with LDS in order to circumvent unreliable manifest difference scores (Nesselroade et al., 1980), the latent difference did not show a significant variance across persons in some cases. In study 3 we therefore applied multilevel SEM with single trial data in order to model brain-behavior relationships of FN amplitude differences between experimental conditions (including neutral, fair and unfair proposer) with individual differences in fairness preferences. The first level tested the within-person experimental manipulation effects of the proposer's fairness (unfair, neutral, fair) on eliciting the FN. The second level included between-person variations in the latent factors of fairness preferences and personality (negative reciprocity, prosociality, assertiveness, honesty-humility). Here, we examined whether the fairness condition effect in FN amplitude elicited by the face of the proposer was larger in participants with higher scores in negative reciprocity, prosociality, assertiveness or honesty-humility. Commonly used in educational and developmental areas, multilevel models can also be useful for experimental designs with repeated measurements not involving time (Hoffman & Rovine, 2007).

Another reason for the limited variability of later difference components in the range of the P300 (such as ERE, LRE and FN) is the overlap of adjacent components and the smearing of time-variable components, broadening their shape and diminishing their amplitude. In order to overcome this problem, future work might combine LDS with residue iteration decomposition (RIDE), a new method that allows researchers to separate ERP components on the basis of latency variability in single trials (Ouyang, Herzmann, Zhou, & Sommer, 2011). The component clusters extracted by RIDE might show greater between-condition variance, since they can be corrected for latency variability.

3.2 The use of socio-economic games to study individual differences

Humans differ in the pursuit of their own material self-interest and the value they assign to social goals (Burlando & Guala, 2005; Camerer, 2003; Engel, 2011). The socio-economic games studied in this dissertation exposed inter-individual variance in fairness preferences underlying the conflict between selfish and prosocial tendencies. Using multiple one-shot socio-economic games such as the PD and SVO, study 2 found active cooperation in terms of increasing the joint outcome to be associated with ability to recognize fearful face expressions and the tendency to be more emotionally expressive. As discussed in section 2.2 we interpreted these findings in line with existing research in that prosocial individuals are more sensitive to the distress of others (Marsh et al., 2007) and more expressive, possibly fostering reciprocal interactions with like-minded others (Schug et al., 2010). Study 3 on the other hand resulted in prosocial individuals showing stronger negative reciprocity quantified by higher rejection rates of unfair offers in UG. Moreover, negative reciprocity predicted individual differences in the FN, a neural indicator of social evaluation. These findings suggest that fairness consideration affects early stages of social evaluation. Altogether the results of study 2 and 3 reveal a heterogeneity of behavior in socio-economic games that is indicative for individual differences in basic affective and cognitive processes. As Zhao and

Smillie (2015) point out, this inter-individual variation can also be partially explained by personality constructs such as dispositional sensitivities to gain and loss (Corr & McNaughton, 2012) and tendencies towards social dominance and affiliation such as assertiveness (Yamagishi et al., 2012), and honesty-humility (Ashton & Lee, 2008).

Socio-economic games are well-controlled and replicable behavioral paradigms, bridging the gap between economic game theory and naturalistic data. They offer a reliable and valid alternative to self-report measures when studying broad and fuzzy personality constructs such as prosociality or trustworthiness (Camerer & Fehr, 2004). Importantly, their simple experimental design allows for statistically powerful manipulations. Experimental manipulations can be carried out by changes in relative pay-offs and by the introduction of additional (economic) variables such as certainty of pay-offs (Charness & Rabin, 2002; Sally, 1995). In Psychology, a greater interest lies on effects of psychological states such as for example mood (Harle & Sanfey, 2007, 2010) or social signals (Mussel, Hewig, Allen, Coles, & Miltner, 2014) on cooperation behavior. The games are described in an objective manner with abstract language and pay-off examples to depict strategies rather than concrete descriptions like “helping” or “trusting”. Abstract language is used to prevent framing effects or violations of the principle of description invariance (Camerer & Fehr, 2004). Small changes in the experimental procedures, especially in terms of social cues, can trigger large changes in results. For example, Andreoni and Rao (2011) experimentally manipulated, which player in a dyadic DG could speak and found that whenever the recipient spoke, giving behavior increased. Furthermore, Haley and Fessler (2005) discovered that people act more cooperatively when a pair of eyes is shown at the location of the computer screen where a bargaining partner makes an allocation. Lastly, also the group size of participants in a given game affects cooperation behavior. If the average impact on another individual declines (as there are more decisions to take), so does the propensity to behave in a more prosocial manner

(Stahl & Haruvy, 2006). These findings question the external validity of measurements of cooperation behavior in neutrally framed laboratory games (Levitt & List, 2007).

However, when studying individual differences in socio-economic choices, the paradigms allow investigating whether or not experimental manipulations affect the correlational structure of the dispositional variables. In line with the outlined interactionistic account of biopsychological personality research (see section 1.1, Stemmler & Wacker, 2010), the situational context and its subjective representation by the participants should moderate the trait–physiology relationships. In study 2 the feedback about the co-player's decision to cooperate or defect in PD moderated the relationship between prosociality and spontaneous emotion expression in that prosocial participants expressed more positive emotion after learning about cooperation, but more negative emotion after being confronted with defection. In study 3 the fairness of the proposer in UG moderated the relationship between negative reciprocity and relative FN, in that participants with high negative reciprocity had a more pronounced relative FN. Future research should try to further disentangle the differential effects of state and trait variables onto socio-economic choices. For instance Riepl, Mussel, Osinsky, and Hewig (2016) investigated the influences of state affect (temporal emotions induced by a short video clip) and trait affect (longer-lasting emotional dispositions) onto responder behavior and ERPs in UG. High trait negative affect led to more pronounced FN amplitudes when participants were in an angry mood, but not if they currently experienced fear or happiness. Their findings suggest that the relationship between trait variables and behavior or neuronal correlates in socio-economic games is dependent on situational context. Future research should therefore incorporate strong experimental manipulation within socio-economic games in order to increase shared variance between interpersonal traits and cooperation behavior also in laboratory settings.

3.3 The representative brain

A recent project conducting replications of 100 psychology studies reported low reliability and reproducibility of studies in psychology (Open Science Collaboration, 2015), a problem that has also recently been discussed in neuroscience (Button et al., 2013; Ioannidis, 2005). Using high power designs with the original material, the Open Science Collaboration found the mean effect size of the replication to be half the size of the mean effect size of the original psychology article. The project revealed especially low percentages of replications in social psychology due to weaker original effects in this domain. The authors concluded that variation in the strength of the original evidence (such as original p value) better predicted replication success than the variation in the characteristics of the researchers conducting the research (such as expertise and experience). While publication and reporting biases are found to be partly responsible for low reproducibility since publications emphasize and reward positive findings, another reason for the inflated effect sizes are small sample sizes since they lead to low statistical power of a study. The statistical power of an experiment is the probability that the null hypothesis will be correctly rejected when it is false (Cohen, 1992). Statistical power is dependent on the significance criterion (such as $\alpha < .05$), the sample size (N), and the effect size in the population (ES). The lower the power of a study, the lower the probability that a discovered effect that passes the required threshold of declaring its observation (that is a criterion such as $\alpha < .05$) actually reflects a true effect (Ioannidis, 2005). Even when a study with low power detects a true effect, it is likely that the estimate of the effect size reported by that study will be exaggerated. Therefore, Button et al. (2013) claim that small sample sizes undermine the reliability of neuroscience. They report the average statistical power of neuroscience studies to be very low which leads to an overestimation of effect size and low reproducibility of results. Importantly, not only small sample size poses a problem but also unrepresentative samples, undermining findings regarding brain–behavior mechanisms. This is why E. B. Falk et al. (2013) argue to promote research in the domain of population neuroscience in order to shed light on a representative brain by providing generalizability of findings with large sample sizes. They suggest increasing the representativeness of samples using neuroimaging approaches in order to account for the inter- and intra-individual variance in neuroscientific data. While experimental psychology or neuroscience often study changes in means due to treatments, the inter- and intra-individual variability among organisms observed by a differential perspective bears fundamental principles of life which ought to be part of modern life science. Hence, E. B. Falk et al. (2013) promote different areas of emphasis within a population neuroscience framework: First they suggest collecting larger samples at multiple time points (by merging existing data sets and meta-analyses) in order to increase replicability and generalizability of results. Second, they propose emphasizing a larger social context and experience as a predictor and moderator of brain-behavior links, such as hyperscanning, whereby the neural activity of two participants interacting is recorded simultaneously, in order to augment ecological validity. Third they advocate collaborations between neural and social scientists. Their rationale being that neuroscience can gain from increased focus on samples and on contextual effects, while population science can gain from increased understanding of brain as mediator of context-behavior links.

The introduction of this dissertation outlined a collaboration between philosophical stances and psychometric models which offers an empirically testable and sound mathematical foundation for the reduction problem. The neuroscientific studies included into this dissertation provide an important step in the right direction for the investigation of brain-behavior relationships in contemporary life science. We applied multivariate modelling with sufficiently large samples in order to investigate individual differences in socio-emotional functions using paradigms borrowed from behavioral economics. Additionally, we collected genetic data which was not the scope of the dissertation but can help us to understand the influence of nature versus nurture in the established brain-behavior relationships. Future projects should clarify to which extent the associations between interpersonal traits and EPRs are based on genetic and environmental influences. The discussion about studying individual differences in socio-economic games (section 3.2) emphasized the importance of broader context and culture. Ignoring variables such as linguistic framing and cultural norms (see also the discussion of study 3 in the attached manuscript) leads to the assumption of uniform brain-behavior relationships which are unlikely. While behavioral economists have a long time considered anonymous laboratory settings to be the gold standard for studying socio-economic decisions, modern Neuroeconomics placed emphasis on the influence of psychological context and culture on cooperation behavior. Interestingly, this change in methodology brought along a change in perception in that the homo oeconomicus has been replaced by the homo empathicus.

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Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt,

1. dass ich die vorliegende Arbeit selbständig und ohne unerlaubte Hilfe verfasst habe,
2. dass ich mich nicht anderwärts um einen Doktorgrad beworben habe und noch keinen Doktorgrad der Psychologie besitze,
3. dass mir die zugrunde liegende Promotionsordnung vom 3. August 2006 bekannt ist.

Berlin, den

Laura Kaltwasser

Original Articles

I. Kaltwasser, L., Hildebrandt, A., Recio, G., Wilhelm, O., & Sommer, W. (2014). Neurocognitive mechanisms of individual differences in face cognition: A replication and extension. *Cognitive, Affective, & Behavioral Neuroscience, 14*(2), 861-878. doi: 10.3758/s13415-013-0234-y

II. Kaltwasser, L., Hildebrandt, A., Wilhelm, O., & Sommer, W. (under review). On the Relationship of Emotional Abilities and Prosocial Behavior. *Evolution and Human Behavior*.

III. Kaltwasser, L., Hildebrandt, A., Wilhelm, O., & Sommer, W. (submitted). Behavioral and neuronal determinants of negative reciprocity in the ultimatum game. *Social Cognitive and Affective Neuroscience.*