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What influences the neural correlates of social cognition?

Studies from a microscopic and macroscopic perspective

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LIST OF ABBREVIATIONS

ACC	Anterior cingulate cortex
aToM	Affective ToM
CN	Cultural neuroscience
CR	Call rate
DLPFC	Dorsolateral prefrontal cortex
dmPFC	Dorsomedial prefrontal cortex
ER	Emotion recognition
ERP	Event-related potential
FFG	Fusiform gyrus
fMRI	Functional magnetic resonance imaging
FP	Face processing
gPPI	Generalized psychophysiological interactions
HC	Healthy participants
IAT	Implicit association task
IFG	Inferior frontal gyrus
MNS	Mirror neuron system
MOG	Middle occipital gyrus
mPFC	Medial prefrontal cortex
PPC	Posterior cingulate cortex
pSTS	Posterior superior temporal sulcus
QC	Quality control
ROI	Region of interest
RTs	Reaction times
SCS	Self-construal scale
SNP	Single-nucleotide polymorphism
SPQ	Schizotypal personality questionnaire
ToM	Theory of mind
TPJ	Temporoparietal junction
VS	Ventral striatum

1 INTRODUCTION

Social cognition plays a fundamental role in all social interactions. It helps us to recognize our interaction partners, understand their emotions, empathize with them and predict their behaviors. These social-cognitive abilities, however, vary among individuals and groups, but the reasons for such variations, especially with regard to neural mechanisms, are not fully understood, yet. One prominent factor which is highly associated with these differences in social cognition is mental illness. For example, a group of studies could demonstrate that schizophrenia is accompanied by pronounced functional impairments in a wide range of social processes (Green, Horan, & Lee, 2015; Mier & Kirsch, 2015). Schizophrenia risk factors can also be found in the general population, such as schizotypy (Fonseca-Pedrero et al., 2014) and schizophrenia risk alleles (Chapman et al., 2018). It has been suggested that the aberrant neural responses to social cognition might vary with schizotypy and schizophrenia risk alleles in healthy participants (Y. Wang et al., 2015). Another prominent factor with potentially critical influence on social cognition is culture. With the development of cultural neuroscience (CN), there is an increasing interest in cultural effects on the neural representation, and behavior during social cognition (Han et al., 2013; Kim & Sasaki, 2014). By directly comparing the neural and behavioral responses of participants with different cultural backgrounds, studies in cultural neuroscience achieved huge successes (Chiao, 2010; Han, 2018; Han et al., 2013) in increasing our knowledge on cultural effects on social cognition.

This dissertation is dedicated to the investigation of inter-individual differences in the neural representations of social cognition from a systematic perspective including a) a microscopic perspective on the individual and b) a macroscopic perspective on the culture. The microscopic perspective refers to the investigation of alteration in neural activation during social cognition with pathological risk factors (such as personality traits and genetic risk alleles) in healthy participants from the same ethnicity. With the macroscopic perspective, cultural effects on the neural responses to social cognition were examined with participants form different cultures.

Before reviewing the current state of the literature on differences in social cognition from the micro- and macroscopic perspective a brief overview of the concept of social cognition and its neural correlates will be presented.

1.1 Social cognition

Social cognition has been defined as a series of mental operations underlying social interactions, which encompasses a wide range of social processes, from basic concepts, like the perception of social cues (social attention), to higher-order social processes, such as empathy and mentalizing (Happé, Cook, & Bird, 2017). The past decades have witnessed a snowballing of interest in the cognitive and neural mechanism of social cognition, raising interest in the factorial structure of social cognition. Based on reviewing the developmental neuroscience of atypical social cognition, Happe & Frith (Happé & Frith, 2014) drew a hypothetical network encompassing a number of components, such as agent identification, emotion processing, empathy, self-processing, and in-/out-group categorization. Green and colleagues (Green et al., 2015) reviewed the references regarding social cognition in schizophrenia and conceived four general social-cognitive processes: (1) perception of social cues, (2) experience sharing, (3) mentalizing, and (4) experiencing and regulating emotions. The National Institute of Mental Health's research domain criteria[1] has recently also divided the domain of social cognition into four constructs: (1) affiliation and attachment, (2) social communication, (3) perception, and (4) understanding of self, perception, and understanding of others. Since these proposals regarding the structure of social cognition present little consistency, this dissertation uses the conceptualization of a meta-analysis (Han & Ma, 2014) viewing social cognition as two broader domains: social-cognitive and social-emotional processing. Specifically, social-cognitive processing includes tasks related to affiliation, self-processing, theory of mind (ToM) and imitation, while those associated with empathy and emotion recognition have been subsumed under social-emotional processing.

As social cognition covers a wide range of social processes, several brain regions grouped together under the term "social brain" are involved on the neural level. These

[1] National Institute of Mental Health's research domain criteria: RDoC, *https://www.nimh.nih.gov/research/research-funded-by-nimh/rdoc/constructs/social-processes.shtml*

regions, again, can be categorized into different networks, such as the mirror neuron system (MNS), mentalizing network, and self-reference network. In despite of the involvement of these brain networks in both social-cognitive and social-emotional processing, they still place extra emphasis on different domains of social cognition. Mirror neurons were initially discovered in the premotor area F5 of macaque monkey and fire both when an animal performs an action and when it obverses another animal (or the experimenter) performing the same or a similar action (Rizzolatti & Craighero, 2004). In the human brain, mirror neurons are assumed to mainly reside in the inferior parietal lobe, the premotor cortex (i.e. BA 44 with BA 6) and the caudal part of the inferior frontal gyrus (IFG) (Cattaneo & Rizzolatti, 2009). From an information-processing perspective, the MNS also includes the superior temporal sulcus (STS) which is responsible for processing the visual and auditory sensory streams (McGarry, Pineda, & Russo, 2015; Pineda, 2008). Although activation in the MNS has been firstly observed during imitation, (Iacoboni et al., 1999), more evidence demonstrated the closer associations of the MNS with social-emotional processes. For example, a group of studies underlined the importance of the MNS in visual and auditory emotion recognition (McGarry et al., 2015; Mier, Lis, et al., 2010; Van der Gaag, Minderaa, & Keysers, 2007) and different kinds of empathy (Gazzola, Aziz-Zadeh, & Keysers, 2006; Krautheim et al., 2019; Lassalle et al., 2018). The so-called mentalizing network has been proposed to include the dorsomedial prefrontal cortex (dmPFC), medial prefrontal cortex (mPFC), posterior cingulate cortex (PPC), temporoparietal junction (TPJ), and posterior superior temporal sulcus (pSTS) (Frith & Frith, 2006). The activation in regions of this network are mainly associated with social-cognitive processing, in particular inferring others' minds (Mier et al., 2012; Mier, Lis, et al., 2010; Mier, Sauer, et al., 2010). Given that people unconsciously make reference to their self during social processes (Sui, 2016), self-related processing plays a significant role either in social-emotional or in social-cognitive processes. The self-reference network is assumed to be linked to the self-related processing and covers the brain regions of mPFC and PPC (Meer, Costafreda, Aleman, & David, 2010). Substantial studies have shown that these regions activated during self-related categorization (Molenberghs, 2013; Molenberghs & Morrison, 2014), traits evaluation (Zhu, Zhang, Fan, & Han, 2007), emotion recognition (Herbert, Herbert, & Pauli, 2011) and ToM (Adams Jr et al., 2010).

1.2 The microscopic perspective: The association of pathological risk factors in healthy participants with social cognition

Social-cognitive impairments have been repeatedly revealed in a number of mental illnesses (Baron-Cohen, 2000; Green et al., 2015). As the pathological risk factors of these mental disorders, such as personality traits and genetic risk alleles, distribute in the healthy population and exert negative influences on behavior in social interactions (Combs & Penn, 2004; Schreiter, Pijnenborg, & Aan Het Rot, 2013), in the present dissertation they are considered as one of most powerful impact factors affecting social cognition from the microscopic perspective on the individual.

Since schizophrenia, as one of the most-disabling conditions among all mental diseases, consistently is association with a variety of deficits in social cognition, the effects of schizophrenia risk factors on social cognition is extensively investigated (E. E. Walter, Fernandez, Snelling, & Barkus, 2016). However, research targeting at exploring whether and how schizophrenia risk factors influence the neural responses to social cognition in healthy samples is still limited.

Two popular approaches to evaluate the impact of schizophrenia risk factors in healthy populations are schizotypy and schizophrenia genotype. Schizotypy is a personality disorder within the schizophrenia spectrum, spreading widely throughout the healthy population (Nelson, Seal, Pantelis, & Phillips, 2013). Accumulating evidence suggests schizotypy sharing common genetic (Roussos et al., 2013), neuroanatomical (Ettinger, Meyhöfer, Steffens, Wagner, & Koutsouleris, 2014), and neurocognitive (Siever & Davis, 2004) abnormalities with schizophrenia. Schizotypy has been categorized into three sub-threshold psychotic symptoms, including positive symptoms, negative symptoms, and disorganization. In terms of schizophrenia genotype, *rs1344706*, a single-nucleotide polymorphism (SNP) in the gene *ZNF804A* (Steinberg et al., 2011; Williams et al., 2011), has been identified in whole-genome association studies as a common genetic variant associated with schizophrenia (O'donovan et al., 2008; Riley et al., 2010). A body of findings demonstrated negative correlations of variations in *rs1344706* with the neural basis of executive functioning (Esslinger et al., 2009) and social cognition (H. Walter et al., 2011). More importantly, with this approach, the schizophrenia endophenotype can be investigated. Endophenotype refers to a quantitative biological trait which is used to build the connections between the

occurrence of well-documented phenotypes and the invisible genetic variabilities, such as SNPs (Gottesman & Gould, 2003).The primary advantage of discovering endophenotypes in schizophrenia is that more potential diagnoses presented with similar phenotypes can be distinguished, making contributions to the clinical reclassification which can advance the prevention and the intervention of schizophrenia (Mohnke et al., 2014; H. Walter et al., 2011). Thus, this dissertation enrolled both schizotypy and schizophrenia risk allele (*rs1344706 SNP*) as the indexes from the microscopic perspective on the individual to investigate its influence on social cognition. In addition, the findings of this dissertation can also explore the schizophrenia endophenotype contributing to the schizophrenia research.

The following findings of aberrations in social cognition will be reviewed for schizophrenia, as well as the associations of these aberrations with schizophrenia risk factors, starting with changes in behavior.

1.2.1 Behavioral evidence on the associations among social cognition, schizophrenia, and schizophrenia risk factors

Schizophrenia has been consistently been associated with high heritability (Eack et al., 2009). In the past decades, growing evidence has shown pronounced social-cognitive impairments in patients with schizophrenia (Green et al., 2015; Savla, Vella, Armstrong, Penn, & Twamley, 2012). With respect to deficits in social-cognitive processing, patients with schizophrenia present obvious deficits in identifying social cues (see review (Bortolon, Capdevielle, & Raffard, 2015)) and in mentalizing (Bora, Yucel, & Pantelis, 2009). Mentalizing (also known as ToM) refers to the ability to infer other's mental states (including intentions, beliefs, and emotions) (Premack & Woodruff, 1978). A series of meta-analyses (Bora et al., 2009; Savla et al., 2012; Sprong, Schothorst, Vos, Hox, & Van Engeland, 2007) consistently revealed that patients with schizophrenia have difficulties either to understand other's intentions through a cartoon panel or to infer other's beliefs with simply written stories. In terms of deficits in social-emotional processing, schizophrenia patients exhibit a negative bias in emotion recognition, i.e. they are prone to report more negative feelings in response to neutral and pleasant stimuli in comparison to healthy controls (Mier et al.,

2014; Premkumar et al., 2008), reflecting a proneness to the faulty perception of (negative) emotions. Such proneness occurring in fundamentally social processes (social perception) could cause false-positive attribution of emotions and intentions, which may lead to the deficits in complex social processes which depend on the integration of several fundamental social processes, such as emotion regulation (Henry, Rendell, Green, McDonald, & O'donnell, 2008; Horan, Hajcak, Wynn, & Green, 2013) and mentalizing (Mier et al., 2017; Mier, Sauer, et al., 2010). Therefore, study one in present dissertation planned to focus on investigating the possible neural basis of false-positive attribution of emotions and intentions during the processing neutral facial expressions.

Several of the impairments in social cognition discovered in schizophrenia were also replicated in healthy participants varying in schizotypy. In terms of social-cognitive processing, links between schizotypy and performance in mentalizing tasks have been intensively investigated but yielded mixed results. For example, some studies showed poorer mentalizing performance associated with both positive and negative symptoms (Henry, Bailey, & Rendell, 2008), but some revealed such associations only with positive symptoms (Barragan, Laurens, Navarro, & Obiols, 2011; Blain, Peterman, & Park, 2017; Gooding & Pflum, 2011; Pickup, 2006). In addition, some studies reported that they did not find a significant correlation between deficits in mentalizing and schizotypy on the behavioral level (Acosta, Straube, & Kircher, 2019; Fernyhough, Jones, Whittle, Waterhouse, & Bentall, 2008). In comparison to the results from the social-cognitive domain, findings of social-emotional processing demonstrate more stable correlations between the negative bias in emotion recognition and schizotypy scores. Brown and Cohen found individuals with increased schizotypy scores to have a negative bias in labeling neutral faces (Brown & Cohen, 2010). Other studies partially replicated these results and extended this finding with the specification that the negative bias in emotion recognition is correlated with positive symptoms (Eack et al., 2009; van't Wout, Aleman, Kessels, Larøi, & Kahn, 2004). Further, such a negative bias in emotion recognition has been discovered in studies on emotion recognition from vocal information as well (Wickline, Nowicki, Bollini, & Walker, 2012), which was also associated with positive symptoms (Shean, Bell, & Cameron, 2007). In short, although substantial efforts have been made in examining the effect of schizotypy on social

cognition, there are still some open questions, especially regarding the social-cognitive processes.

In comparison to the association of impairments in social cognition with schizotypy, the genetic effects are even less clear. Based on the limited knowledge, previous studies focused mainly on testing the associations between *rs1344706* and ToM performance, but no significant evidence was directly demonstrated. Walter and colleagues applied a ToM fMRI-task to two independent healthy samples, and both samples showed insignificant differences between *rs1344706* genotype groups in the mentalizing performance (Mohnke et al., 2014; H. Walter et al., 2011). This result has also been replicated by Hargreaves and colleagues who conducted two traditional ToM tasks with a large-scale sample size (Hargreaves et al., 2012). However, the study of Hargreaves and colleagues revealed that the risk allele of the *rs1344706* SNP was significantly correlated with interpersonal attribution scores, indicating risk carriers presenting a tendency to attribute negative events to other people (Hargreaves et al., 2012). Although little direct evidence proved genetic effects on social-cognitive performance on the behavioral level in general (Rasetti & Weinberger, 2011), several studies found robust *rs1344706* effects on the neural response during social cognition (Gurung & Prata, 2015), which underlines the necessity of investigating the correlations between schizophrenia risk factors and social cognition with neuroscientific approaches.

1.2.2 Neural evidence on the associations among social cognition, schizophrenia, and schizophrenia risk factors

The past decades have witnessed a tremendous expansion in the use of neuroscientific methods to study alterations in social cognition in schizophrenia. Substantial studies, comparing schizophrenia patients with healthy controls, have consistently revealed neural aberration during social-cognitive and social-emotional processing in schizophrenia. The most-extensively studied domain of social-cognitive processing in schizophrenia is mentalizing. Considerable studies continuously reported hypoactivation in brain regions responsible for mentalizing in schizophrenia (Jáni & Kašpárek, 2018; Kronbichler, Tschernegg, Martin, Schurz, & Kronbichler, 2017). For instance, compared to healthy controls, patients with schizophrenia showed

hypoactivation in the TPJ and mPFC while inferring others' beliefs (Dodell-Feder, Tully, Lincoln, & Hooker, 2014; J. Lee, Quintana, Nori, & Green, 2011); hypoactivation in the mPFC and orbitofrontal cortex (OFC) while taking others' perspectives (Eack, Wojtalik, Newhill, Keshavan, & Phillips, 2013); and reduced activation in TPJ and IFG while watching animated sequences regarding social interaction presented by geometric figures (Das, Lagopoulos, Coulston, Henderson, & Malhi, 2012). However, this pattern of hypoactivity in the mentalizing network and MNS during mentalizing tasks seems to be observed in a reversed fashion for processing non-emotional and non-intentional social stimuli. A study of Walter and colleagues revealed a reduced difference in STS activation in schizophrenia patients during the ToM and the control condition in a social cognition task (H. Walter et al., 2009). This result has been replicated in the study of Ciaramidaro and colleagues with the same ToM task (Ciaramidaro et al., 2014). Results of Ciaramidaro and colleagues further demonstrated enhanced connectivity from the right STS to IFG in the control task in patients with schizophrenia (Ciaramidaro et al., 2014). With another social cognition task Mier and colleagues also consistently revealed aberrant STS functioning during control condition in schizophrenia patients in comparison to healthy participants (Mier et al., 2017; Mier, Sauer, et al., 2010). These findings of hyperactivity in the mentalizing network in response to the non-intentional social scenes fit with the proneness to over-attribute intention to others in schizophrenia, which is called hyper-mentalizing (Abu-Akel, 1999, 2000; Crespi & Badcock, 2008).

Regarding the social-emotional processing, a large number of studies has concentrated on investigating how individuals with schizophrenia perceive and process facial emotions. Previous meta-analyses revealed that, compared to healthy participants, schizophrenia patients presented hypoactivation in regions including the amygdala, anterior cingulate cortex (ACC) and MFC (H. Li, Chan, McAlonan, & Gong, 2009; Taylor et al., 2012); and hyperactivation in the cuneus, parietal lobule and STS (Taylor et al., 2012). Notably, Anticevic and colleagues observed decreased amygdala activation in response to aversive social stimuli relative to neutral social stimuli in schizophrenia patients in comparison to healthy controls, but such amygdala hypoactivation was not found when activation in response to the condition that the neutral facial expression was not subtracted from the response to negative facial expression (Anticevic et al., 2010). This finding demonstrates that the amygdala

hypoactivation in schizophrenia during contrasts of emotional versus neutral faces might be attributed to the hyperactivation in the amygdala for processing neutral stimuli (Green et al., 2015; Mier & Kirsch, 2015), suggesting that the neutral stimuli might have been considered as salient or threats to patients with schizophrenia (Adolphs, 2003; Mier et al., 2014).

There is a growing number of studies also revealing the association between schizotypy and social cognition on the neural level (Cohen, Mohr, Ettinger, Chan, & Park, 2015). Regarding social-cognitive processing, previous studies discovered associations of higher self-reported schizotypy scores with increased activation in the pSTS while processing self-related stimuli (Arzy, Mohr, Michel, & Blanke, 2007); with deactivation in the dorsal ACC while viewing pictures of social rejection (Premkumar et al., 2012); and with altered pSTS activity while mentalizing (Abu-Akel, Apperly, Wood, & Hansen, 2017; Y. Wang et al., 2015). In terms of neural correlates of the social-emotional processing domain, schizotypy has been found associated with decreased activation in the PPC and pSTS in response to happy faces (Huang et al., 2013); and with amygdala deactivation, while processing fearful faces (Y. Wang et al., 2018). Wang and colleagues further reported links between higher schizotypy scores and reduced brain connectivity from amygdala to the mPFC for processing fearful faces, and to dorsal ACC for happy faces (Y. Wang et al., 2018). Although substantial findings support the association of schizotypy with aberrant brain functioning during social cognition, there is no consensus that such altered neural responses to social cognition are determined or associated with one specific domain of schizotypy. For example, in the mentalizing domain, two fMRI studies both found associations of schizotypy with altered pSTS activity for mentalizing in healthy population (Abu-Akel et al., 2017; Y. Wang et al., 2015). However, one pointed to the importance of positive symptoms in altered neural responses to mentalizing (Abu-Akel et al., 2017), and the other highlighted the role of negative symptoms (Y. Wang et al., 2015). Thus, more empirical evidence is needed to clarify the correlations of the different domains of schizotypy with the specific social process.

In terms of the genetic effects on the neural response to social cognition, previous genetic imaging studies demonstrated a huge interest in social-cognitive processing (particularly in mentalizing), which achieved relative reproducible results. Walter and

colleagues first explored the *rs1344706* effect on the neural representation of social-cognitive processing with a ToM task (H. Walter et al., 2011). They found that the schizophrenia risk allele was linked to decreased activation during ToM in mPFC, tempo-parietal cortex, inferior parietal cortex, posterior cingulate and lateral PFC in healthy participants. In line with this finding, Mohnke and colleagues reported decreased activation in the TPJ, dmPFC and PPC associated with *rs1344706* in another healthy sample (Mohnke et al., 2014). They further observed a significant risk allele dose effect on increased functional connectivity of the left TPJ with IFG. In addition, *rs1344706* effects on social-emotional processing were reported as well. Esslinger and colleagues employed an emotional face-processing task and revealed increased connectivity of the right amygdala with the parietal and temporal cortices, hippocampus and striatum associated with the risk allele in a healthy sample (Esslinger et al., 2009). These findings shed lights on the importance of *rs1344706* for the neural responses during social cognition (Chang, Xiao, & Li, 2017), but more efforts are still required.

Taken together, deficits in social cognition has been well documented in schizophrenia (Green et al., 2015; Mier & Kirsch, 2015), and can vary with schizophrenia risk factors in healthy samples (Chang et al., 2017; Cohen et al., 2015). Given that the schizophrenia factors correlated with a wide range of neural correlates of social cognition, this dissertation applied a social cognition task including three types of social cognition, from neural face perception, over emotion recognition, to inferring others' mind (Mier et al., 2017; Mier, Sauer, et al., 2010) to healthy participants for comprehensively investigating differences in the neural and behavioral correlates of social cognition with regard to the microscopic level. With the social cognition task, Mier and colleagues reached fruitful achievement in schizophrenia research. They found hypoactivation in pSTS in schizophrenia patients during emotion recognition and mentalizing in comparison to healthy controls (Mier et al., 2017), and observed patients with schizophrenia presenting hyperactivity of pSTS during neutral face processing (Mier et al., 2017; Mier, Sauer, et al., 2010). These findings provide more evidence to the hypothesis of deficits in mentalizing in schizophrenia, especially in line with the idea that the hyper-mentalizing occurring in response to social stimuli without emotional, or intentional meaning. Thus, the present dissertation attempted to replicate these findings from Mier and colleagues in healthy participants with distinct risk factors

of schizophrenia (namely schizotypy and *rs1344706*) in study 1, allowing to exam whether the pSTS hyperfunctioning for neutral face processing presents an endophenotype in schizophrenia unconfounded of medication status or chronicity of disease, making contribution to advance the understanding of the underlying mechanism of schizophrenia. In addition, using such an approach may testify the microscopic perspective to better understand the neural basis of social cognition.

1.3 The macroscopic perspective: the neural correlates of social cognition and culture

Given that human's capacities are not only based on biological inheritance but are in large parts subject to cultural influence (Tomasello, 1999), considerable empirical evidence suggests that culture has a significant impact on human's social cognition (Elfenbein & Ambady, 2003). Prior to addressing the associations between social cognition and culture, it is necessary to understand the definition of culture, especially to know about the associations between the concepts of culture, ethnicity, race, and nationality, which are introduced as follows.

1.3.1 Culture, ethnicity, race, and nationality

In line with Bates and Plog (Bates & Plog, 1990), culture refers to "a system of shared beliefs, values, customs, behaviors, and artifacts that members of a society use to cope with their world and with one another, and that are transmitted from generation to generation through social learning" ((Bates & Plog, 1990), p.7). One of the most popular and significant cultural differences is between individualism and collectivism that are assumed to reflect different dimensions of cultural values (F. Li & Aksoy, 2007). Individualism is prominent in the western countries, especially in the US and in European countries, and encourages self-identity that is rather independent of social contexts and of others. In contrast, collectivism is more prominent in East Asia, such as in China, Japan, and Korea, and emphasizes fundamental social connections, resulting in an interdependent view of the self and partial overlap in the representation

of the self and close others (Markus & Kitayama, 2010). Empirical studies underpin this cultural variance by showing differences in social cognition between cultures.

For better understanding, the specific effects of culture, measuring cultural values has been proposed as a relatively effective manner (Chiao et al., 2010). However, based on limited knowledge, only a few studies considered cultural values as indexes of cultures. This leads to a common limitation in most cross-cultural studies that differences between cultures are assumed to be represented by differences among race, nationality, and ethnicity, and in consequence, these concepts are often used synonymously and are not well disentangled. In study two of this dissertation, participants were strictly selected to reach homogenous samples according to ethnicity, race, nationality, and culture. These concepts are defined in the following (Figure 1).

Ethnicity refers to a group of people having common cultural traits that they use to distinguish themselves from other ethnic groups. The members of an ethnic group share common customs and traditions, language, sense of history, and so forth (Jones, 1997). However, in comparison to cultures, ethnic groups are not fixed, bounded entities, they are open, flexible, and subject to change (Barth, 1998; Smedley & Smedley, 2005). Nationality refers to a legal relationship between an individual person and a nation, and it emphasizes an individual's political nature (Vonk, 2012). In some cases, if a nation is constituted by a single ethnicity, its nationality can define its citizenships' ethnicity, such as in Japan. However, given that a nation usually is constituted by multi-ethnic groups, such as in America, it is hard to define a citizenships' ethnicity only based on his/her nationality (Smith, Fischer, Vignoles, & Bond, 2013). Race, a term frequently used in daily discourse and social perception, refers to a group of people who share the physical traits, ancestry, and genetic background. However, the agreement among most researchers in evolutionary biology and anthropology is that there is no biological evidence for the existence of separate human races (Segall, 2002). Thus, race has even been considered as a concept which is not scientifically meaningful (Allen, 1994). In consequence, the concept 'ethnicity' instead of 'race' is used in the present dissertation.

However, since the concepts are often neither rigorously defined, nor sufficiently separated, for a comprehensive review in the field of CN, I will present those with a theoretical background on culture, ethnicity, nationality, and race in the following introduction together under the umbrella of cultural effects.

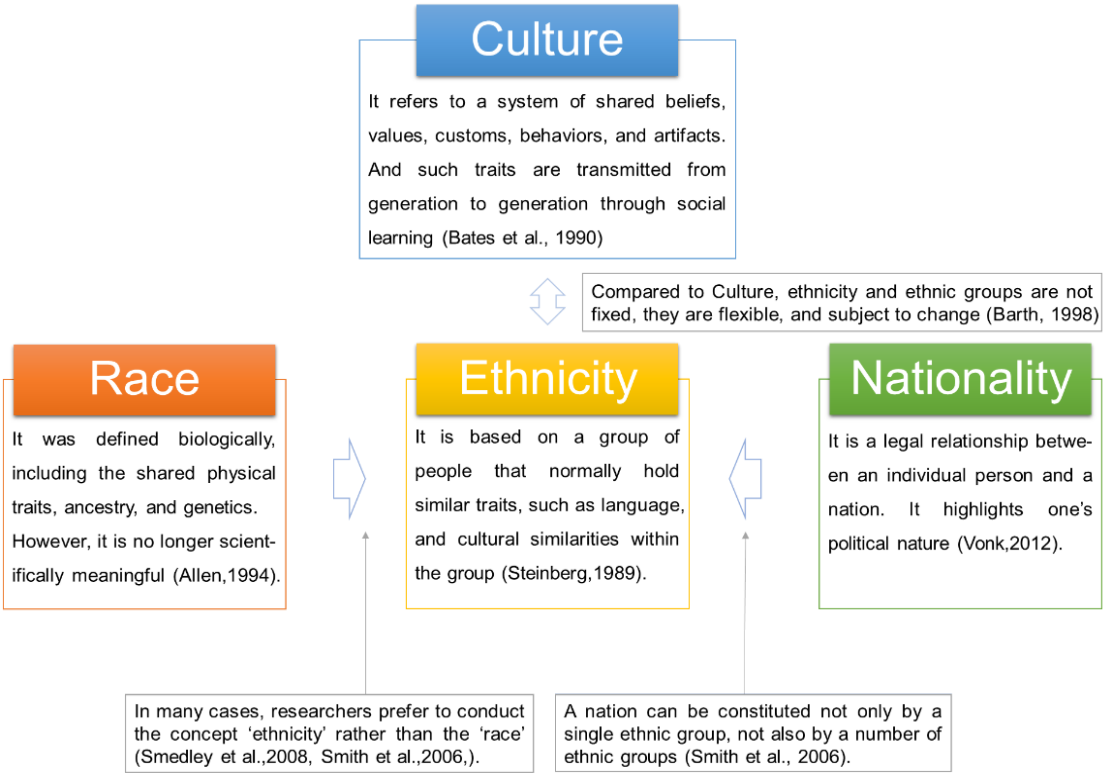


Figure 1. The relationship between culture, race, nationality, and ethnicity

1.3.2 Social cognition and culture

In terms of the influence of culture on social cognition, a number of studies have mainly focused on the so-called intracultural advantage and discussed whether such an effect is valid across cultures.

1.3.2.1 Intracultural advantage and its subcategory

The intracultural advantage illustrates the phenomenon that individuals show better performance for recognizing and processing social information expressed by someone of their own culture than of another culture (Elfenbein & Ambady, 2003). Notably, such an effect also presents in a seemingly paradoxical pattern during face processing. Ge

and colleagues (Ge et al., 2009) designed a well-controlled facial-processing task including both a recognition and a categorization task with Caucasian and Chinese facial stimuli and applied it to British and Chinese participants. They found that, compared to own-ethnicity faces, both cultural groups *recognized* other-ethnicity faces slower and with lower accuracy, whereas shorter reaction times were needed for *categorizing* other-ethnicity faces in both groups. Such effect that people are faster to categorize a face from another-ethnicity than from their own-ethnicity is referred to as other-ethnicity categorization advantage (Levin, 1996; Valentine & Endo, 1992) which has been consistently reported with distinct cultural samples (Ge et al., 2009; Zhao & Bentin, 2008, 2011).

The intracultural advantage has been revealed in several domains of social cognition. Concerning social-cognitive processing, Adams and colleagues (Adams Jr et al., 2010) applied the “reading the mind in the eyes test” to Japanese and Americans and found that both cultural groups showed better ToM performance for persons of their own culture than of the other culture. The intracultural advantage was also reported by a more recent study (Ng, Steele, Sasaki, Sakamoto, & Williams, 2015) with an ethnicity-based recognition task. The results showed that Caucasians were faster in recognizing people from their own ethnicity than from the other ethnicity (East Asian).

Regarding social-emotional processing, Johnson and colleagues (Johnson et al., 2002) used a judicial decision-making task in Caucasians and found that participants reported greater feelings of empathy with people from the own ethnicity as opposed to another ethnicity. Comparable results were found in individuals with a collectivistic background. Cheon and colleagues (Cheon et al., 2011) applied an empathy task to evaluate empathy for the psychological pain of ethnicity-based in-group and out-group member in Korean participants and found significantly more empathy for the in-group relative to the out-group pain. Regarding emotion recognition, Elfenbein and Ambady (Elfenbein & Ambady, 2003) found that Caucasians showed higher accuracy and shorter response times for recognizing emotional expression performed by Caucasians than by Asians. The results are in line with an earlier meta-analysis across 48 behavioral studies (Elfenbein & Ambady, 2002), showing higher accuracy for emotion recognition when emotions are both expressed and recognized by participants of the same ethnic background.

Although these findings provide strong evidence for an intracultural advantage in many aspects of social cognition, there is also evidence demonstrating that this phenomenon is modulated by the specific culture. Lee and colleagues applied an emotion recognition task to Chinese participants and found that Chinese participants performed more accurate at recognizing anger, disgust, and sadness when the emotion expressors were from other-ethnicity then from their own-ethnicity, reflecting a reversed advantage of emotion recognition in Chinese (S. L. Lee, Chiu, & Chan, 2005). This finding was replicated by a study of Prado and colleagues, they found an intracultural advantage of emotion recognition in the Australian group, but a reversed advantage in the Chinese group (Prado et al., 2014). The reversed advantage of emotion recognition was not only found in Chinese, but it has also partially replicated in Japanese samples. Chiao and colleagues (Chiao et al., 2008) found that Caucasian participants were significantly more accurate at recognizing fear in own-cultural than other-cultural faces, reflecting the intracultural advantage in the Caucasian group. However, they found that the Japanese group demonstrated shorter response times for recognizing fearful faces of another ethnicity than of their own ethnicity. To summarize, the current state of the literature suggests an intracultural advantage in individualistic sample but presents an inconsistent pattern in the collectivistic samples, warranting more empirical evidence.

1.3.2.2 Cultural neuroscience studies on social cognition

CN is a term which was coined by Chiao and Ambady (Chiao & Ambady, 2007) referring to an interdisciplinary field combining the concepts and methods from cultural psychology, neurosciences, and neurogenetics together. It is dedicated to explain mutual constitution of culture and neurobiological basis by investigating the interactions among cultural factors, genetic variants, and brain function (Chiao, 2010; Han et al., 2013). Over the past decade, cultural neuroscientists started paying more attention to cultural differences in the functioning of the social brain with remarkable progress (Han & Ma, 2014; Kim & Sasaki, 2014). One of the most interesting endeavors of cultural neuroscience is how human brain activity is tuned by culturally familiar/unfamiliar social information. In this regard, increasing evidence indicates

apparent cultural differences in brain functioning in terms of social-cognitive and social-emotional processing.

In terms of social-cognitive processing, Liew and colleagues (Liew, Han, & Aziz - Zadeh, 2011) conducted an fMRI study with Chinese participants watching culturally familiar/unfamiliar gestures from a number of video clips. They found culturally familiar gestures resulting in activation in the PPC, dmPFC, and TPJ. These regions are linked to the neural circuit engaged in mentalizing (Frith & Frith, 2006). Interestingly, culturally unfamiliar gestures activated regions of the inferior parietal lobe, superior frontal gyrus, and superior parietal lobe, which are involved in automatic motor simulations of observed actions and have been linked to the mirror neuron system (Rizzolatti & Sinigaglia, 2010). A more recent study on the imitation of gestures (Losin, Iacoboni, Martin, Cross, & Dapretto, 2012) found increased activation in regions associated with the mirror neuron system when European Americans imitate or observe meaningless gestures performed by someone of their own ethnicity in comparison to the gestures performed by someone of another ethnicity. These findings indicate that cultural experiences may result in specific neural mechanisms in the human brain that code culturally familiar information, further suggesting that cultural backgrounds play a crucial role in social-cognitive processing.

Several studies showed that the cultural background also influences how one represents oneself with respect to close others. In this context, self-construal refers to the construction of self-concept, and to the extent the self is defined independently of or interdependently with others (Cross, Hardin, & Gercek-Swing, 2010). Zhu and colleagues (Zhu et al., 2007) applied a trait-judgment fMRI-task to examine cultural differences in the neural activity underlying self-construal with western and Chinese participants. Participants were required to make trait judgments of oneself, a close other (i.e. one's mother), and a well-known celebrity. Results showed increased activation in the ventral mPFC during trait judgments of oneself versus a celebrity across all participants. However, trait judgments of one's mother, but not of a celebrity, activated the mPFC in Chinese but not in Westerners, reflecting a shared neural basis of the self and a close other in Chinese which might imply individuals from collectivism are more interdependent with close others. This has been further supported by a study of Chiao and colleagues (Chiao et al., 2009). They applied a judgment task containing

two kinds of self-descriptions (general and contextual self-descriptions) in Japanese and Americans and found that Americans had higher mPFC activity for the general than for the contextual self-descriptions, whereas Japanese presented the same neural response to contextual rather than general self-description. These findings from functional brain imaging suggest that relative to an individualistic culture, the self in a collectivistic culture is more interdependent with others.

Cultural differences in self-definitions were also found in certain cultural value-related priming studies. Sui and colleagues (Sui, Hong, Liu, Humphreys, & Han, 2013) recorded ERPs from British and Chinese adults during judgments of orientations of one's own and a friend's face after they were primed with independent and interdependent self-construal. Results showed that priming an interdependent self-construal reduced the default anterior N2 (which is related to cognitive control and mismatch, see (Folstein & Van Petten, 2008)) in response to their own faces for British, whereas priming an independent self-construal suppressed the default anterior N2 in response to their friend's face for Chinese participants. These findings probably not only provide evidence for people with different cultural backgrounds differentiating in self-definition, but also illustrate that culture can be learned by individuals, and then, influence their original neural mechanism of self-construal. Another study, supporting the idea that social learning can modulate cultural effects, used priming of independent and interdependent self-construal to Chinese participants before applying a gambling task (Varnum, Shi, Chen, Qiu, & Han, 2014). The authors found higher activation in the ventral striatum (VS) in response to winning money for the self than for a friend when an independent self-construal was primed, but priming an interdependent self-construal resulted in increased activation in VS in response to winning money for the self and for a friend. These findings indicate that cultural values, even within one cultural group, can be changed by social learning (priming), respectively by changing the focus of reference (individualism versus collectivism).

With respect to social-emotional processing, cultural values might also have a crucial impact on the neural mechanism of social-emotional processing, such as empathy and emotion recognition.

Regarding empathy, cultural neuroscientists are interested in the cultural differences in the neural mechanism for empathizing with persons of the own versus another ethnicity. Cheon and colleagues (Cheon et al., 2011) used cross-cultural neuroimaging to investigate neural responses while Korean and American participants observed scenes of ethnicity-based in-group and out-group members in emotional pain. In both groups, participants showed higher TPJ activity while observing the emotional pain of in-group versus out-group members, and this effect was stronger for Koreans than Americans. Moreover, another study (de Greck et al., 2012) applied an empathy task to examine cultural differences in the neural responses of empathy for anger in Chinese and German participants. They found that while empathizing with own-cultural anger faces, the Chinese group showed activation in the left dmPFC, whereas the German group showed activation in the right TPJ, right STS, and left middle insula. Those regions activated in Chinese participants are closely linked to emotion regulation (Etkin, Büchel, & Gross, 2015), and those observed in Germans are typically involved in empathy and emotion processing (Olsson & Öhman, 2009). These findings suggest that social-emotional information may be processed through different neural paths between cultures, possibly resulting in different psychological responses.

Interestingly, recent studies also pointed out the social learning effect existing in social-emotional processing. Scholars believe that social learning happens when one is exposed to another cultural background, leading to facilitate the process of integration. Derntl and colleagues (Derntl, Habel, et al., 2009) assessed the neural responses for recognizing Caucasian emotional faces in Asian and European males. The authors found a significant negative correlation between duration of stay in a foreign culture and amygdala activation for recognizing emotional faces versus neutral faces in Asians, suggesting that exposure to another's culture affects the neural response to facial expressions of emotions. A more recent study by the same group (Derntl et al., 2012) including participants of both genders replicated these findings, providing further evidence on such social learning effect on social-emotional processing.

Taken together, culture may modulate the neural representations of social-cognitive processing and social-emotional processing. Based on the idea that the aberrations in higher-order social cognition might be based on impaired fundamental social-cognitive processes, the cultural differences in different domains of social interaction might be

also caused by distinct strategies of basic social-cognitive processes (such as social categorization) between cultures. However, studies on the direct comparison between two cultures in terms of basic social-cognitive processes are still missing. Thus, the second study of the present dissertation planned to focus on investigating the cultural differences in categorizing basic social cues (neutral facial expression) with a social categorization task in Chinese and German samples with respect to the macroscopic level. In addition, individuals' core cultural values are not invariable and constant. Such values could be altered by social/cultural learning which might happen in a subtle way, such as exposure to the opposite cultural background or intercultural communication. The consequences of such social learning effect may impose an influence on individuals' social-cognitive and social-emotional processes, which probably could reduce the intracultural advantage in social cognition (Derntl, Habel, et al., 2009; Derntl et al., 2012). Thus, study two of the present dissertation involved both Chinese and German samples in Germany, resulting in the possibility to investigate the social learning effect on basic social-cognitive processes in the Chinese group.

1.4 Aims

The primary aim of this dissertation is to promote the understanding of the neural mechanism of social cognition from the microscopic and the macroscopic perspective: the individual and the group. In terms of investigating the neural mechanism of social cognition from the individual perspective, self-reported schizotypy and genetics analyses were used in combination with fMRI to reveal whether the neural correlates of different domains of social cognition vary with schizotypy and *rs1344706* in healthy participants from the same ethnicity (Study one). In study two, from the group perspective, a social-categorization task with Caucasian and Asian stimuli was applied to two groups of participants recruited in Germany with different cultural backgrounds (China and Germany). In this way, the effect of an intracultural advantage in the neural bases of a fundamental social process (social categorization) and its possible cultural differences can be examined. In addition, social learning effects on the intracultural advantage in the neural correlates of social categorization can be investigated within the Chinese group.

2 STUDY ONE: UNDERSTANDING THE NEURAL CORRELATES OF SOCIAL COGNITION FROM THE MICROSCOPIC PERSPECTIVE: THE INDIVIDUAL

2.1 Hyperfunctioning of right posterior superior temporal sulcus in response to neutral facial expressions presents an endophenotype of schizophrenia[2]

2.1.1 Abstract

Deficits in social cognition have been proposed as a marker of schizophrenia. Growing evidence suggests especially hyperfunctioning of right posterior superior temporal sulcus (pSTS) in response to neutral social stimuli reflecting the neural correlates of social-cognitive impairments in schizophrenia. We characterized healthy participants according to schizotypy (*n = 74*) and the single-nucleotide polymorphism *rs1344706* in *ZNF804A* (*n = 73*), as they represent risk factors for schizophrenia from the perspectives of personality traits and genetics, respectively. A social-cognitive fMRI-task was applied to investigate the association of right pSTS hyperfunctioning in response to neutral face stimuli with schizotypy and *rs1344706*. Higher right pSTS activation in response to neutral facial expressions was found in individuals with increased positive (trend) and disorganization symptoms, as well as in carriers of the risk allele of *rs1344706*. In addition, a positive association between right-left pSTS connectivity and disorganization symptoms during neutral face processing was revealed. We suggest that right pSTS hyperfunctioning in response to neutral facial expressions presents an endophenotype of schizophrenia. We assume that this right pSTS hyperfunctioning presents a vulnerability to perceive neutral social stimuli as emotionally or intentionally salient.

[2] Manuscript submitted: Yan, Z., Schmidt, S. N.L., Frank, J., Witt, S. H., Hass, J., Kirsch, P. & Mier, D. (submitted). Hyperfunctioning of right posterior superior temporal sulcus in response to neutral facial expressions presents an endophenotype of schizophrenia. Manuscript submitted for publication.

2.1.2 Introduction

Social-cognitive impairments have been proposed to present a marker of schizophrenia (Abu-Akel, 1999, 2000; Crespi & Badcock, 2008; Derntl & Habel, 2011). The impairments occur in different domains of social cognition, ranging from deficits in neutral face processing (Holt et al., 2006; Mier et al., 2017), emotion recognition (Derntl, Finkelmeyer, et al., 2009), up to complex social-cognitive processes (Brüne, 2005), like inferring others' mental states, known as theory of mind (ToM) (Premack & Woodruff, 1978), and are highly important for social functioning (Couture, Penn, & Roberts, 2006). The association of these deficits to enhanced activity and connectivity of the right posterior superior temporal sulcus (pSTS, (Mier et al., 2017; Mier, Sauer, et al., 2010)), makes aberrant pSTS functioning during social cognition a highly promising endophenotype candidate for schizophrenia.

For investigating the neural correlates of social-cognitive impairments in schizophrenia, we (Mier, Lis, et al., 2010) developed a social-cognitive task that assesses several aspects of social cognition (namely neutral face processing (FP), emotion recognition (ER), and affective ToM (aToM)) using emotional facial expressions as stimuli. Applying this task, we found hyperactivity in the right pSTS during FP, but not during aToM in two independent samples of schizophrenia patients (Mier et al., 2017; Mier, Sauer, et al., 2010). Further, we found hypo-connectivity between right and left pSTS for aToM, and a relative hyper-connectivity between right and left pSTS for FP (Mier et al., 2017). Other authors also (Ciaramidaro et al., 2014; Straube, Green, Sass, & Kircher, 2013) showed hyper-connectivity of the pSTS in emotionally and intentionally neutral conditions of social-cognitive paradigms. Since the pSTS is one core area of social cognition and prominently involved in inferring other's intentions (Gallagher & Frith, 2003), enhanced pSTS activation during FP might be interpreted as a vulnerability for false-positive perceptions of intentions, also called hyper-mentalizing (Mier & Kirsch, 2015).

Imaging genetics studies with healthy participants (HC) and with relatives of schizophrenia patients provided further evidence for aberrant pSTS functioning during social cognition as an endophenotype of schizophrenia. *Rs1344706*, a single-nucleotide polymorphism (SNP) in the gene *ZNF804A* (Steinberg et al., 2011; Williams et al., 2011) was identified in whole-genome association studies as a common genetic

variant associated with schizophrenia (O'donovan et al., 2008; Riley et al., 2010). *Rs1344706* is involved in regulating gene expression (Chapman et al., 2018), and has been linked to executive functioning (Esslinger et al., 2009) and social cognition (H. Walter et al., 2011). Imaging genetics findings from two healthy samples suggest that activity and connectivity of the STS and adjacent temporoparietal junction are associated with variation in *rs1344706* in a mentalizing task with sketches (Mohnke et al., 2014; H. Walter et al., 2011). Further, healthy relatives of schizophrenia patients showed aberrant activation in this task. Family members had reduced activation in the medial prefrontal cortex during mentalizing, but enhanced activation in posterior cingulate cortex and right middle temporal gyrus. Interestingly, activation in right middle temporal gyrus during mentalizing correlated positively with self-reported paranoid ideation (Mohnke et al., 2015). This finding is exemplary of the approach to identify endophenotypes by investigating variances of traits of a disease in HC.

Schizotypy as part of the schizophrenia spectrum is a valuable construct that refers to personality structures spreading dimensionally throughout the population (Ettinger et al., 2015; Nelson et al., 2013), but can also present as a personality disorder (Association, 2013). Schizotypy can be characterized by a three-factor model of sub-threshold psychotic symptoms, including positive (e.g., ideas of reference), negative (e.g., no close friends), and disorganization symptoms (e.g., eccentric behavior). Accumulating evidence suggests schizotypy and schizophrenia have common genetic (Roussos et al., 2013), neuroanatomical (Ettinger et al., 2014), and neurocognitive (Siever & Davis, 2004) abnormalities. Additionally, differences in schizotypy traits has been associated with different kinds of social-cognitive deficits (Abu-Akel et al., 2017; Sacks, de Mamani, & Garcia, 2012).

To date, only two fMRI studies have investigated the association between neural correlates of mentalizing and schizotypy in HC. Both studies found right pSTS activity for mentalizing varying with schizotypy (Abu-Akel et al., 2017; Y. Wang et al., 2015). However, whereas one (Y. Wang et al., 2015) revealed negative symptoms to be positively related to right pSTS activation during mentalizing, the other (Abu-Akel et al., 2017) showed a positive association with positive symptoms. Since these studies used different stimulus materials (ToM cartoon stories with sketches of situations, and a competitive game again with sketches of materials of the rock, paper, scissor game),

the question arises whether right pSTS functioning varies more consistently with schizotypy in response to inherently social stimuli, such as faces. A general and crucial aspect when comparing social-cognitive studies, however, is not only the selection of stimulus material, but also of the control condition (ranging from emotionally neutral analogues of the experimental condition to completely non-social conditions), which is usually subtracted from the higher-order social-cognitive process. Therefore, divergent findings in prior studies might be explained by differences in brain activation in the control condition between participants with and without schizophrenia risk.

To summarize, deficits in social cognition are proposed to present a marker for schizophrenia (Derntl & Habel, 2011), and aberrant pSTS functioning during social cognition is a promising endophenotype of schizophrenia (Mohnke et al., 2014; H. Walter et al., 2011). In the present imaging genetics study, we applied a social-cognitive fMRI-task (Mier et al., 2017; Mier, Sauer, et al., 2010) that assesses different social-cognitive processes, and has constantly revealed right pSTS hyperactivation during FP, but not during mentalizing, in patients with schizophrenia (Mier et al., 2017; Mier, Sauer, et al., 2010). We aimed to replicate our previous findings from schizophrenia samples in HC, depending on the *ZNF804A rs1344706* risk allele and schizotypy to assess the possibility of pSTS hyperfunctioning unconfounded of medication status, or chronicity of disease. For both *ZNF804A rs1344706* risk allele and schizotypy, previous studies found a relationship to aberrant pSTS activation during mentalizing (Abu-Akel et al., 2017; Mohnke et al., 2014; H. Walter et al., 2011; Y. Wang et al., 2015), but the response to neutral facial expressions was not investigated. We hypothesized that activation and connectivity of right pSTS in response to neutral facial expressions in HC is positively associated with 1) the risk allele of the *rs1344706* genotype and 2) higher self-reported schizotypy.

2.1.3 Material and Methods

2.1.3.1 Participants

Of 81 healthy participants, seven were excluded for the present analyses: five due to low fMRI data quality, two due to anomalies in their self-report questionnaires. For the genetics analyses, one additional participant was excluded because genotyping for *rs1344706* was not possible. Therefore, we included 74 participants (40 females, see Table 1) in the behavioral and imaging analyses and 73 participants (39 females) for the imaging genetic analyses. Participants were grouped for the imaging genetics analysis for the existence of the risk allele of schizophrenia (O'donovan et al., 2008); *ZNF804A* genotype groups: 62 AA/CA (risk allele carriers and 11 CC non-risk allele carriers). All participants were of German ancestry, had higher school certificate, were right-handed, had normal or corrected-to-normal vision and no self-reported background of mental or neurological disorders, or drug abuse. In addition, participants reported having no relatives with schizophrenia, or bipolar disorder.

Table 1 Characteristics of the sample

	Whole Sample (n=74)		Range of SPQ scores (n=74)		AA/CA (n=62)		CC (n=11)		Genotype effect	
	Mean	SD	Min	Max	Mean	*SD*	Mean	*SD*	*t*	*p*
Age	23.50	3.83	-	-	23.27	3.80	24.36	3.98	-.87	.387
SPQ total	11.00	9.09	0	37	11.54	9.08	7.82	9.28	1.25	.215
Positive symptoms	5.05	4.86	0	21	5.18	4.93	4.09	4.68	.68	.500
Negative symptoms	3.05	3.17	0	13	3.29	3.31	1.82	2.14	1.42	.226
Disorganization symptoms	2.89	2.92	0	12	3.08	2.93	1.90	2.91	1.22	.215

Note: SPQ, Schizotypal Personality Questionnaire; AA/CA indicates the risk allele carriers; CC indicates the non-risk-allele carriers.

Prior to the study, participants were informed about study procedure and purpose and gave their written informed consent. The study was approved by the local ethics board of the Medical Faculty Mannheim, University of Heidelberg. The data reported here is part of a larger study on the human mirror neuron system that involved a measurement containing simultaneous EEG-fMRI with 3 tasks (including an imitation task, an empathy task, and the social-cognitive task presented here), blood-taking and a series of questionnaires, including the Schizotypal Personality Questionnaire (SPQ (Raine, 1991), details are presented in the Supplementary Text 1), and a second measurement with transcranial magnetic stimulation prior to fMRI. Results reported in this manuscript are based on the fMRI data of the first appointment.

2.1.3.2 Experimental paradigm

We applied a modified version of the social-cognitive task that was used in earlier studies with schizophrenia patients (Mier et al., 2017; Mier, Sauer, et al., 2010). The paradigm was extended to four conditions including three levels of social cognition [lower-level social cognition (FP), ER, and higher-level social cognition (aToM)], and a non-social control condition. In each trial of the social-cognitive conditions, a statement preceded a facial expression. These statements described the facial expressions referring to physical features (gender or age) for FP, the emotional state (fear or anger) for ER, or the possible intention (running away or blustering) for aToM. For FP, only neutral facial stimuli were shown, for ER and aToM only emotional facial expressions. The facial stimuli were taken from the Karolinska Directed Emotional Faces set (Goeleven, De Raedt, Leyman, & Verschuere, 2008). Half of the stimulus persons were male, and the same persons were used for each of the social-cognitive conditions. For the control condition, prior to a geometric figure (a triangle or a circle) a statement describing the figure (e.g., “This is a circle”) was displayed. Task duration was around 8 minutes (details of timing and presentation can be found in Figure 1 and Supplementary Text 2).

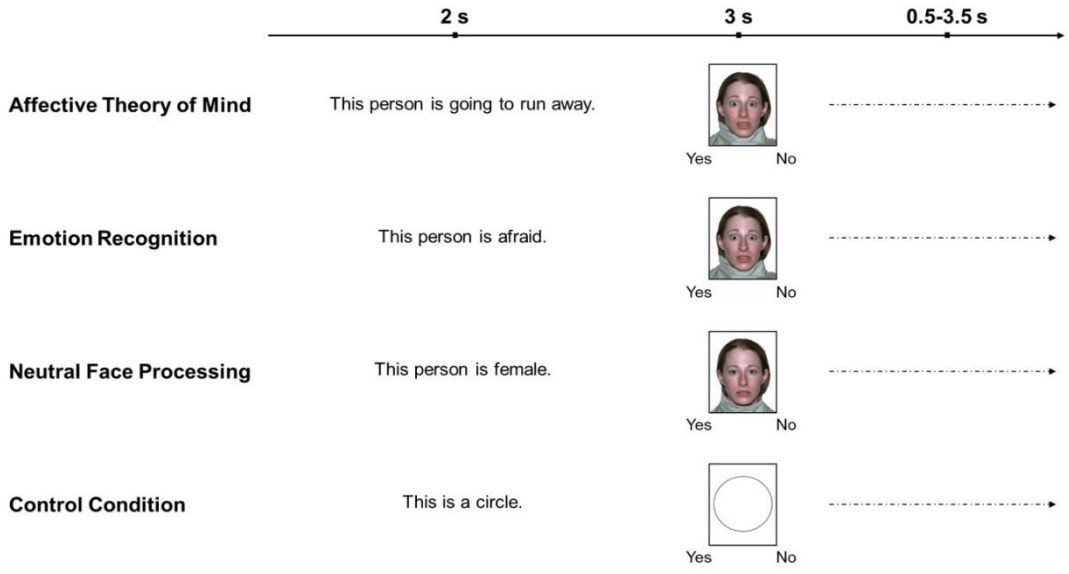


Figure 1. The social cognition fMRI task.

2.1.3.3 Genotyping

Genotypes for *ZNF804A SNP rs1344706* were extracted from whole genome genotype data obtained using Illumina Global Screening array and following stringent quality control (see Supplementary Text 3).

2.1.3.4 Imaging Data acquisition and analyses

The study was conducted with a 3 Tesla Siemens Tim TRIO whole-body magnetic resonance tomography (Siemens Medical Systems, Erlangen, Germany; acquisition protocol can be found in Supplementary Text 4). Brain activity and connectivity analyses were conducted with SPM8 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, UK). Data preprocessing contained slice time correction, realignment, co-registration to the structural image, spatial normalization (MNI template) with resampling to a 3 x 3 x 3 mm voxel size, and spatially smoothing with an 8 mm full-width half-maximum kernel. The first level analyses were achieved by a general linear model with four regressors (aToM, ER, FP, control), and six motion parameters, derived from the realignment procedure, as covariates. The time series was high-pass filtered using a 128 Hz function. From the model, linear combinations of the regressors built the contrasts of interest, including effects of each higher against the lower social-cognitive condition (aToM > ER, ER > FP), and each condition against control (aToM > control, ER > control, FP > control). Connectivity analyses were applied using generalized psychophysiological interactions (gPPI (McLaren, Ries, Xu, & Johnson, 2012)), as implemented in the gPPI toolbox (http://www.nitrc.org/projects/gppi) with a functional mask of right STS as seed region, produced from our previous comparison between aToM and ER in 40 undergraduate students (Mier, Sauer, et al., 2010) (details of the gPPI analysis are reported in Supplementary Text 4).

For second-level analyses, significance threshold for exploratory whole-brain analyses was $p < .05$ FWE-corrected, $k = 10$. We conducted one sample t-tests to analyze the effect of each social-cognitive condition, and a within-subject one-way analysis of variance (ANOVA) to identify the neural correlates of increased social-cognitive processing (contrast: [aToM > Control] > [ER > Control] > [FP > Control]). Regression

analyses were conducted to explore the associations between the factors related to schizophrenia (schizotypy and the *rs1344706* risk allele) and right pSTS activation, and connectivity for the different social-cognitive conditions. Region of interest (ROI) analyses (significance threshold $p_{FWE} < .05$ *small volume corrected (svc), k = 10*) were applied for right, and also left pSTS.

Behavioral data were analyzed with SPSS version 23. Differences between the social-cognitive conditions in reaction times (RTs) or accuracy were analyzed with repeated measures ANOVA, post-hoc tests were conducted with paired-samples t-tests. Pearson correlation was applied to investigate possible associations among task conditions, and to test the associations between schizotypy and task performance. We conducted independent sample t-tests to test genotype effects on task performance, as well as to investigate differences in self-reported schizotypy, depending on genotype.

2.1.4 Results

2.1.4.1 Behavior

Similar to our previous studies (Mier et al., 2017; Mier, Sauer, et al., 2010), RTs and accuracy differed significantly between conditions, with the control condition being the easiest and aToM being the most difficult task condition. Neither genotype nor schizotypy significantly affected task performance (detailed behavioral results are reported in Supplementary Text 5, and Supplementary Figure 1). In addition, no significant differences in self-reported schizotypy were revealed, depending on the risk-allele (see Table 1).

2.1.4.2 Imaging

Replicating results from our previous studies (Mier et al., 2017; Mier, Sauer, et al., 2010), activation increased linearly from FP over ER to aToM in regions of the "social brain", including bilateral superior temporal gyrus covering pSTS, bilateral inferior frontal gyrus covering BA44 (Figure 2; detailed results of task effects are presented in Supplementary Table 1). Whole brain analyses of right pSTS connectivity differences between conditions were not significant across participants. ROI-analyses revealed greater pSTS connectivity between hemispheres for aToM compared to ER at trend level (peak voxel: -57, -49, 7; t = 3.37, p_{FWE} =.069 svc, k = 10).

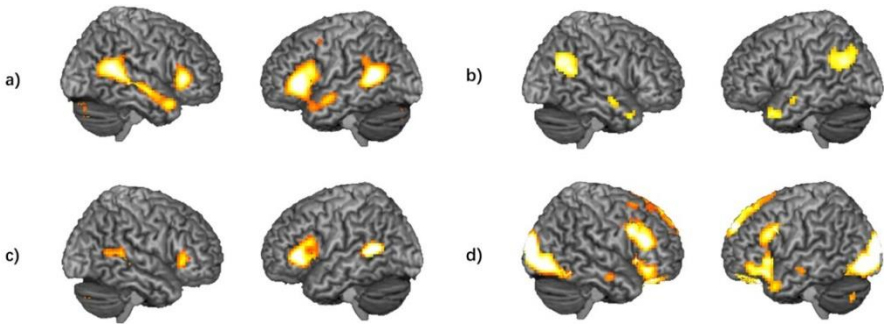


Figure 2. Neural correlates of distinct social-cognitive processes. a) neural correlates of increasing social-cognitive demands [with the contrast: (Affective Theory of Mind > control) > (emotion recognition > control) > (neutral face processing > control)]; b) affective Theory of Mind (> emotion recognition); c) emotion recognition (> neutral face processing); d) neutral face processing (> control condition). Significance threshold is p < .05, FWE-corrected, k = 10.

2.1.4.2.1 rs1344706

Risk allele carriers compared to non-risk-allele carriers had increased right pSTS activation during FP (> control; peak voxel: 63, -58, 13; *t* = 3.19, p_{FWE} = .042 svc, *k* = 10, Figure 3). Neither for ER, nor for aToM, were significant differences in pSTS activation found.

2.1.4.2.2 Schizotypy

There was a trend for a positive association between right pSTS activation for FP (> control) and schizotypy sum score (peak voxel: 63, -55, 10; t = 3.01, p_{FWE} = .065 svc, *k* = 10). There was also a significant positive association between activation in right pSTS and disorganization symptoms (peak voxel: 57, -55, 7; *t* = 3.54, p_{FWE} =.018 svc, *k* = 10, Figure 3), and at trend level with positive symptoms (peak voxel: 63, -55, 10; *t* = 3.94, p_{FWE}=.077 svc, *k* = 10, Figure 3). ROI analysis also revealed a significant positive correlation between disorganization symptoms and right-left pSTS connectivity during FP (> control; peak voxel: -45, -70, 22; *t* = 3.60, p_{FWE} =.038 svc, *k* = 10, see Figure 3). Neither for ER, nor for aToM, were significant associations between schizotypy and pSTS activation, or connectivity found.

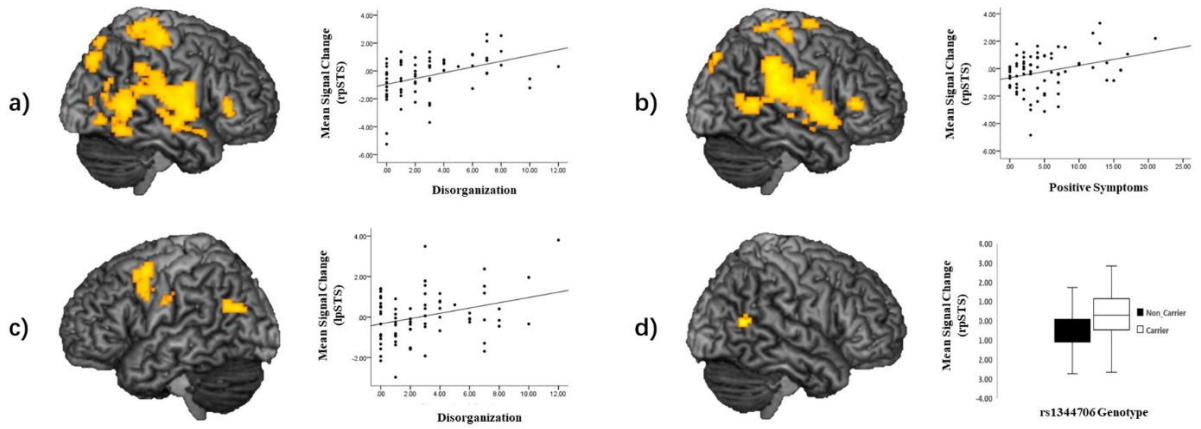


Figure 3. Associations between functioning of right posterior superior temporal sulcus for neutral face processing and schizotypy as well as *rs1344706* genotype. The first two scatter plots show positive correlations between activation in the right posterior superior temporal sulcus (pSTS) for neutral face processing (> control) and disorganization (a), as well as positive symptoms (b); c) positive association of disorganization with right to left pSTS connectivity for neutral face processing (> control); d) genotype effect of increased activation in right pSTS for neutral face processing (> control). Significance threshold for display purposes is p < .005 uncorrected, k = 10. Note: rpSTS stands for right posterior superior temporal sulcus, lpSTS stands for left posterior superior temporal sulcus.

2.1.5 Discussion

The present study aimed at investigating whether pSTS functioning during social-cognitive processing is an endophenotype for schizophrenia. Confirming our hypothesis, we found a positive association of right pSTS activation for neutral face processing with schizotypy (in particular disorganization, and positive symptoms on a trend level), and also with a risk allele for schizophrenia. Furthermore, connectivity between right and left pSTS during neutral face processing was positively associated with disorganization symptoms.

The pSTS is consistently found to be involved in inferring goals and intentions (Gallagher & Frith, 2003; Mier et al., 2017; Mier, Sauer, et al., 2010). Across participants, we replicated our previous findings showing decreased performance and enhanced activation in pSTS and BA44 with increasing social-cognitive demands. With this, our results again highlight the role of pSTS functioning for inferring others' intentions (Gallagher & Frith, 2003). Importantly, enhanced right pSTS functioning in our participants with schizophrenia risk allele and subclinical symptoms of schizophrenia was present only for neutral face processing, but not for higher order social-cognitive conditions. This supports our previous findings and conclusions that in particular basic social-cognitive processes are affected in schizophrenia which might in turn cause the frequently observed impairments in higher-order social cognition in this disorder (Mier et al., 2017; Mier, Sauer, et al., 2010). Our results are also consistent with further previous findings with schizophrenia patients. A recent study reported not only increased pSTS activation in response to the emotionally and intentionally neutral control condition in their social-cognitive task but also enhanced pSTS connectivity (Ciaramidaro et al., 2014). These results add to the idea that pSTS dysfunction for neutral social stimuli might be regarded as neural basis for hyper-mentalizing, which may constitute a vulnerability to the emergence of delusion (Mier et al., 2017).

Kapur (Kapur, 2003; Kapur, Mizrahi, & Li, 2005) proposed that psychosis, particularly delusions, result from aberrant attribution of novelty and salience to objects and associations, and that faulty attributions of salience arise due to chaotic, context-inappropriate firing of dopamine neurons. Delusions have been suggested to represent a deficit in encoding the precision of predictions and prediction errors (Corlett, Taylor,

Wang, Fletcher, & Krystal, 2010), indicating a bottom-up inappropriate perceptual input; i.e. aberrant salience. Supporting this idea, our results revealed a positive association between positive symptoms (trend), and the risk allele for schizophrenia, with activation in the right pSTS for neutral faces, indicating that people with increased positive symptoms might be prone to perceive neutral faces as emotionally or intentionally salient. Whether these inappropriate perceptual inputs lead to delusions depends on how individuals interpret these false perceptions, demonstrating the importance of a top-down cognitive explanation to delusions (Kapur, 2003; Kapur et al., 2005). Individuals interpret what they perceive according to their memory, expectation and cultural context. However, when the cognitive explanation is interfered or interrupted due to executive dysfunction, the accumulating experiences of aberrant salience might gradually increase confusion and result in delusional ideas. Patients with disorganization present a pronounced deficit in cognitive coordination (Uhlhaas, Phillips, Mitchell, & Silverstein, 2006), making them less able to appropriately interpret the perceptual information (Phillips & Silverstein, 2003), which reflects dysfunction of top-down control. In addition to the marginally significant association between self-reported positive symptoms and enhanced right pSTS activation, we found significant positive associations between disorganization symptoms and right pSTS activation, and connectivity. In our present sample, increased self-reported disorganization symptoms might suggest worsen cognitive coordination, which may in turn reduce top-down control over aberrant perception of neutral facial expressions.

Together, our findings add to the perspective that delusions probably derive from dynamic interactions between bottom-up erroneous perception and top-down cognitive deficits, caused by enhanced responsiveness to emotionally and intentionally neutral social stimuli (Mier & Kirsch, 2015). Since all of our participants were without a history of mental disorders, we found alterations only on the level of neural functioning. Further studies with large patient samples that allow the analysis of subgroups are needed to investigate the validity of the proposed mechanisms in schizophrenia.

Importantly, aberrantly high pSTS functioning in response to neutral social stimuli seems to be not ‘only’ a marker of schizophrenia, but an endophenotype of schizophrenia according to the criteria characterizing an endophenotype proposed by Gottesman and Gould (Gottesman & Gould, 2003): 1) The endophenotype is

associated with illness in the population: Aberrant right pSTS functioning is consistently observed in patients with schizophrenia in response to stimuli and situations without emotional, or intentional meaning (Ciaramidaro et al., 2014; Holt et al., 2006; Mier et al., 2017; Mier, Sauer, et al., 2010; Straube et al., 2013; H. Walter et al., 2009). Our current results show a comparable neural pattern in healthy participants with increased schizophrenic proneness, illustrating an association of right pSTS dysfunction with schizophrenia symptoms also in HC. 2) The endophenotype is heritable: In line with previous studies showing aberrant pSTS functioning in schizophrenia risk-allele carriers (Mohnke et al., 2014; H. Walter et al., 2011), we found enhanced right pSTS activity in response to the neutral condition in *rs1344706* risk-allele carriers, possibly reflecting one aspect of the heredity of the right pSTS dysfunction. 3) The endophenotype should be state-independent: We found the neural pattern first in schizophrenia out-patients who were remitted from positive pathology (Mier, Sauer, et al., 2010), then in in-patients with schizophrenia (Mier et al., 2017), now even in healthy participants carrying the psychosis allele, suggesting that right pSTS dysfunction might represent a state-independent neural pattern for schizophrenia. 4) Within families, endophenotype and illness co-segregate: Increased engagement of right pSTS varied with positive symptoms in schizophrenia patients' relatives (Mohnke et al., 2015), suggesting that right pSTS dysfunction and schizophrenia symptoms co-segregate within families. However, studies systematically investigating differences in pSTS functioning between relatives of schizophrenia patients are pending. 5) The endophenotype in affected family members is found at a higher rate in non-affected family members than in HC: While hyperfunctioning was observed in relatives of schizophrenia patients who reported positive symptoms, it is also found in non-affected family members at a higher rate than in healthy participants without familial risk for schizophrenia (Mohnke et al., 2015). In addition to the criteria proposed by Gottesman and Gould, a further criterion has been put forward (Lenzenweger, 2013): 6) The endophenotype should be a trait that can be measured reliably, and ideally is more strongly related with the disease of interest than with other psychiatric conditions: Aberrant activation in the right pSTS was consistently revealed by our social-cognitive task in schizophrenia patients (Mier et al., 2017; Mier, Sauer, et al., 2010) and also in the current study in healthy participants with increased schizophrenic proneness, but not in patients with borderline personality disorder (Mier et al., 2012). Additionally, especially in schizophrenia patients with paranoid symptoms, pSTS activity during the

neutral condition was higher than in patients with autism (Ciaramidaro et al., 2014; Pinkham, Hopfinger, Pelphrey, Piven, & Penn, 2008), highlighting that dysfunction in right pSTS is not only a reliably assessable trait, but also specific to schizophrenia. Thus, there is extensive evidence supporting the idea that hyperfunctioning of pSTS to neutral social stimuli represents an endophenotype for schizophrenia.

Despite the reported studies consistently finding genotype effects on brain activation and connectivity (Mohnke et al., 2014; H. Walter et al., 2011), they, like the present study, tested only one risk SNP's effect. In addition, since genetic penetrance is higher for endophenotypes than phenotypes (Meyer-Lindenberg & Weinberger, 2006); i.e. significant association between the risk allele and right pSTS functioning, but no significant association between the risk-allele and schizotypy, several approaches would be of interest for future studies to validate our findings and to investigate the proposed mechanisms: a) investigating the load of risk SNPs to reveal biological subcategories of schizophrenia (Ehrenreich et al., 2018), b) due to unequal distribution of risk allele presence (only 11 participant homozygous for the non-risk allele), replication of the finding with pre-selection of participants depending on their genotype, c) replicating the marginally significant association of positive symptoms and right pSTS activation with different approaches to assess schizotypy, such as the Oxford-Liverpool Inventory of Feelings and Experiences (Mason, Claridge, & Jackson, 1995), d) targeting not only right pSTS activation and connectivity, but also of further regions that are central for social-cognitive processing (e.g. amygdala, MPFC). Besides, some previous studies only reported hypo-functioning in the pSTS in patients with schizophrenia in response to higher level social cognition (such as ToM) (Mohnke et al., 2014; H. Walter et al., 2011). Whether these studies would also reveal pSTS hyperfunctioning if the neutral condition was investigated remains an open question. Moreover, some studies proposed aberrations in left pSTS instead of the right pSTS presenting an intermediate phenotype for schizophrenia (Mohnke et al., 2014; H. Walter et al., 2011). Perner and colleagues (Perner, Aichhorn, Kronbichler, Staffen, & Ladurner, 2006) suggested that the left pSTS is linked to perspective differences for mental and non-mental objects, while the right pSTS is associated with mental states. Future studies should approach the question of laterality with a systematic variance of social-cognitive processing to clarify the functioning of this region in schizophrenia.

Taken together, our findings point to right pSTS hyperfunctioning in response to neutral faces representing an endophenotype of schizophrenia. We assume that right pSTS hyperfunctioning presents a vulnerability to perceive neutral social stimuli as emotionally or intentionally salient and suggest that bottom-up and top-down aberrations interact to cause delusions via deficient social perception.

2.1.6 Supplementary materials

2.1.6.1 Supplementary Text 1: Questionnaire

The Schizotypal personality questionnaire (SPQ, (Raine, 1991)) includes 74 items with a dichotomous response format [Yes(1)/No(0)] and consists of nine subscales which represent the DSM-IV criteria for schizotypal personality disorders. The subscales can be grouped by three factors: positive (magical ideation, paranoid ideation, perceptual aberrations, ideas of reference), negative (constricted affect, no close friends, social anxiety), and disorganization (odd speech, eccentric behavior) symptoms. Cronbach's alpha for the whole SPQ in the present study is 0.91, for the subscale of positive symptoms 0.86, for the subscale of the negative symptoms 0.82, for the subscale of disorganization 0.79.

2.1.6.2 Supplementary Text 2: Details of timing and presentation of the social-cognitive task

Each trial started with a statement for 2 s, followed by a picture (a facial expression or a geometric figure) with the choice "yes" or "no" underneath. Participants were asked to respond whether the preceding statement matches the current picture by pressing the corresponding button within 3 s. In 50% of trials, the statement matched the following picture. Trials were separated by a fixation cross of a mean duration of 2 s (with a jitter of 0.5–3.5 s). Each condition had 20 trials resulting in an experimental time of 8 min approximately. The task was implemented with Presentation software, version 9.50 (Neurobehavioral Systems Albany, CA, USA). Participants responded with a current design response device (Current Designs, Inc., Philadelphia, PA) and watched the experiment via VisuaStim video goggles (Resonance Technology Inc, Northridge, USA).

2.1.6.3 Supplementary Text 3: Genotyping

DNA was extracted from full blood using PerkinElmer chemagen (Baesweiler, Germany) chemagic 360 DNA extraction system. Genotyping was performed using Illumina (San Diego, CA, USA) Global Screening Array bead chips. Resulting

genotypes were subjected to stringent quality control (QC). This included removal of DNA samples with either insufficient quality (individual missing rate > 2%, based on prefiltered SNPs with call rate > 0.95), discrepancies between phenotypic and genotype based sex, or heterozogosity deviation (autosomal |FST| > 0.2), and removal of SNPs with insufficient call rate (CR<0.98), deviation from Hardy-Weinberg equilibrium (pHWE < 1x10-6), or low minor allele frequency (MAF < 0.01), as well as removal of genetic outliers. No individual failed QC tests.

For the present study genotypes of SNP *rs1344706* were finally extracted from the quality-controlled data set described above.

2.1.6.4 Supplementary Text 4: Functional imaging data acquisition and analyses

Prior to functional imaging, we acquired a T1-weighted anatomical scan (TR = 1570 ms, TE = 2.75 ms; flip angle = 15°, field of view = 256 mm; matrix = 256x256; voxel size 1x1x1 mm). Functional scans were obtained by conducting a T2*-weighted gradient echo planar imaging sequence (TR = 2000 ms; TE = 30 ms; flip angle 80 degree; field of view = 192 mm; matrix: 64 x 64 mm). Each volume consisted of 32 slices, acquired in a descending order with a slice-thickness of 3 mm with 1 mm gap (voxel size: 3 x 3 x 4 mm^3).

For connectivity analyses of right pSTS connectivity, the first eigenvariate of the seed region was extracted for each person (no significance threshold was applied for eigenvariate extraction), deconvolved with the canonical hemodynamic response function (HRF) and multiplied with time series of each, aToM, emotion recognition, neutral face processing, and control conditions to represent condition-specific interactions. These interaction regressors were subsequently convolved again with the HRF.

2.1.6.5 Supplementary Text 5: Behavioral results

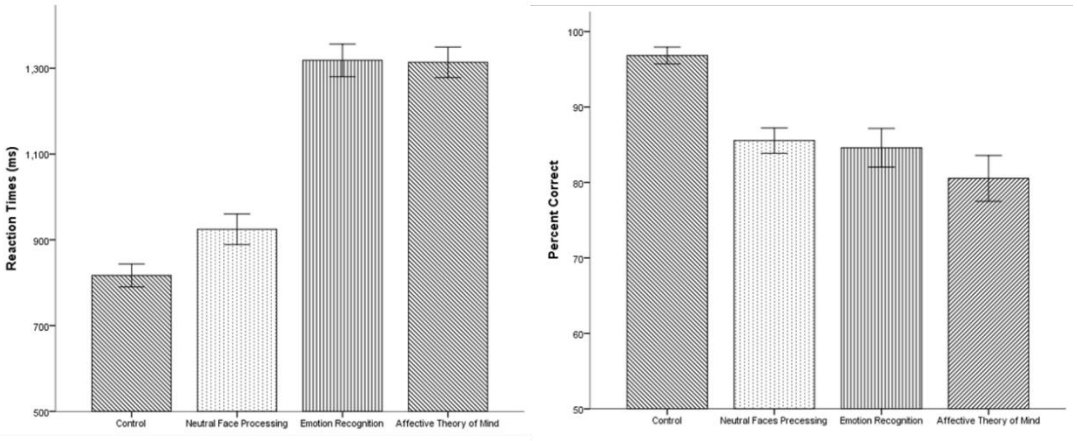
A significant main effect of condition in RTs (F = 465.58, $p < .001$, $\eta^2 = .86$) and in accuracy (F = 44.32, $p < .001$, $\eta^2 = .39$) was found (see Figure 2). Post-hoc tests revealed that the RTs in the control condition were significantly shorter than in the

neutral face processing condition (t (73) = -7.00, p < .001, d = -.81), in the emotion recognition condition (t (73) = -27.84, p < .001, d = -3.24), as well as in the aToM condition (t (73) = -30.68, p < .001, d = -3.57); the RTs in the neutral face processing condition were shorter than in the emotion recognition condition (t (73) = -19.61, p < .001, d = -2.28) and in the aToM condition (t (73) = -20.79, p < .001, d = -2.42). No significant difference of RTs between the emotion recognition condition and the aToM condition was found (t (73) = .35, p = .73). In terms of accuracy, post-hoc tests showed participants presented better performance in the control condition than in the neutral face processing condition (t (73) = 11.34, p < .001, d = 1.32), in the emotion recognition condition (t (73) = 8.75, p < .001, d = 1.02), as well as in the aToM condition (t (73) = 10.73, p < .001, d = 1.25); and lower accuracy in the aToM condition was found in comparison to the neutral face processing condition (t (73) = -2.74, p = .008, d = -.32) and the emotion recognition condition (t (73) = -2.67, p = .009, d = -.31). No significant differences in the accuracy were revealed between neutral face processing and emotion recognition (t (73) = .63, p = .53). Furthermore, correlation analyses only showed a significant association of the accuracy in the aToM condition and in the emotion recognition condition (r = .42, p < .001, d = .94).

No significant performance differences between risk- and non-risk-alle carriers occurred. Also no significant correlations between schizotypy scores and performance were found.

2.1.6.6 Supplementary Figure

Supplementary Figure 1. Behavioral results of the social-cognitive fMRI task. Mean of reaction times (left) and of accuracy (right) for the four experimental conditions.



2.1.6.7 Supplementary Table

Supplementary Table 1. Brain activation in the social-cognitive task across all participants.

Area	L/R	Cluster	MNI			t-value	p-value
			x	y	z		
aToM > ER							
Whole Brain Analyses							
Superior Temporal Gyrus	R	330	63	-52	19	7.60	< 0.001
Superior Temporal Gyrus	L	330	-45	-61	28	7.23	< 0.001
Superior Temporal Gyrus	L	58	-45	17	-29	6.77	< 0.001
Middle Temporal Gyrus	R	15	57	-7	-14	5.80	< 0.001
Superior Temporal Gyrus	R	11	45	14	-32	5.64	< 0.001
Middle Temporal Gyrus	L	11	-60	-7	-11	5.42	< 0.001
Region of Interest Analyses							
Superior Temporal Sulcus	L		-45	-58	22	5.99	< 0.001
Superior Temporal Sulcus	R		63	-52	19	7.60	< 0.001
ER > NF							
Whole Brain Analyses							
Inferior Frontal Gyrus	L	379	-51	32	4	10.22	< 0.001
Superior Temporal Gyrus	L	224	-51	-52	10	9.61	< 0.001
Superior Temporal Gyrus	R	165	45	-40	10	6.73	< 0.001
Inferior Frontal Gyrus	R	79	48	26	-2	6.65	< 0.001
Cingulate Gyrus	L	21	-6	20	46	5.70	0.004
Cerebellum	R	13	27	-76	-38	5.75	0.004
Region of Interest Analyses							
Superior Temporal Sulcus	L		-54	-52	10	9.33	< 0.001
Superior Temporal Sulcus	R		51	-52	10	6.00	< 0.001
NF > Control							
Whole Brain Analyses							
Occipital Lobe	R	2736	12	-97	13	18.39	< 0.001
Frontal Lobe	L	969	-6	59	34	10.32	< 0.001
Inferior Frontal Gyrus	R	536	45	32	16	11.92	< 0.001
Inferior Frontal Gyrus	L	444	-39	23	-17	9.06	< 0.001
Rectal Gyrus	R	381	3	38	-20	11.50	< 0.001
Inferior Frontal Gyrus	R	324	36	32	-11	12.19	< 0.001
Middle Frontal Gyrus	L	216	-42	11	31	9.21	< 0.001
Cingulate Gyrus	L	41	0	-52	28	6.69	< 0.001
Parahippocampal Gyrus	R	37	30	-7	-32	8.14	< 0.001
Parahippocampal Gyrus	R	36	21	-10	-14	8.68	< 0.001

Middle Frontal Gyrus	R	30	36	14	61	6.09	0.001
Cerebellum	L	20	0	-55	-32	7.21	< 0.001
Inferior Temporal Gyrus	R	18	63	-10	-20	6.57	< 0.001
Parahippocampal Gyrus	L	14	-18	-10	-14	6.30	0.001
Middle Temporal Gyrus	L	12	-63	-16	-14	5.71	0.005
Cerebellum	L	11	-9	-79	-32	6.42	< 0.001
Cerebellum	L	10	-33	-70	-44	6.45	< 0.001
Region of Interest Analyses							
Superior Temporal Sulcus	R		51	-61	22	4.91	< 0.001
(aToM > control) > (ER > control) > (NF>control)							
Whole Brain Analyses							
Superior Temporal Gyrus	R	942	48	-37	4	10.88	< 0.001
Inferior Frontal Gyrus	L	712	-51	32	4	12.2	< 0.001
Superior Temporal Gyrus	L	591	-57	-52	10	11.03	< 0.001
Inferior Frontal Gyrus	R	192	54	29	4	9.86	< 0.001
Cerebellum	R	171	27	-73	-35	6.96	< 0.001
Cerebellum	L	72	-21	-79	-32	7.54	< 0.001
Superior Frontal Gyrus	L	60	-3	11	61	5.8	< 0.001
Precuneus	L	27	-6	-67	40	6.26	< 0.001
Cerebellum	L	25	-9	-40	22	5.9	< 0.001
Middle Frontal Gyrus	L	15	-39	5	43	5.34	0.004
Cerebellum	R	12	21	-10	31	5.03	0.013
Region of Interest Analyses							
Superior Temporal Sulcus	L		-57	-52	10	11.03	< 0.001
Superior Temporal Sulcus	R		60	-52	16	9.64	< 0.001

Note: 1. aToM = affective Theory of Mind, ER = emotion recognition, NF = neutral face processing.

2. Significance threshold is $p < 0.05$ *FWE-corrected,* $k = 10$.

3 STUDY TWO: UNDERSTANDING THE NEURAL CORRELATES OF SOCIAL COGNITION FROM THE MACROSCOPIC PERSPECTIVE: THE CULTURE

Results from study one showed positive associations of activation and connectivity of right pSTS during neutral face processing with schizophrenia risk factors in healthy participants, indicating that pSTS functioning during social-cognitive processing presents an endophenotype for schizophrenia. Further, increased right pSTS functioning associated with schizophrenia risk factors in healthy participants was demonstrated only for processing neutral facial expressions, but not for other higher-order social-cognitive task conditions. This finding apparently adds evidence to the idea that basic social-cognitive processes affected in schizophrenia, might in turn lead to of the impairments in higher-order social cognition (Mier et al., 2017; Mier, Sauer, et al., 2010). More importantly, schizotypy and schizophrenia genotype were indexed to represent risk factors for schizophrenia as indicators of the individual level in study one. The associations between them and the aberrations of neural responses during social cognition directly supported the microscopic perspective on the individual that the neural correlates of social cognition are associated with individual factors.

Study two was planned to advance the understanding of neural correlates of social cognition from the macroscopic perspective on the culture. Although there are a few studies that describe the link between neural correlates of social cognition and culture, their results make contribution mostly to associations of culture with neural correlates of higher-order social-cognitive processes (Cheon et al., 2011; Han, 2018; Han et al., 2013), neglecting the possible associations with lower-order social-cognitive processes. Since differences in social interaction between cultures might be rooted in distinct paths or strategies during basic social-cognitive processes, studies that explore culture effects on basic social-cognitive processes are urgently needed.

Social categorization is a fundamental social-cognitive process, which enables individuals to simplify the social environment around them by classifying others into broad groupings according to social coalitions and to predict future social behaviors (Wilder, 1986). It plays an effective and efficient role in navigating the social world (Fiske & Taylor, 2013; Macrae & Bodenhausen, 2001) but it also brings intergroup

comparison and in-group favoritism which might lead to intergroup biases and even conflicts (Hall & Crisp, 2005). In-ethnicity bias, based on ethnicity-based social categorizations is one of the most prevalent and powerful in-group biases, which has been linked to the causes of ethnic prejudice and stereotypes (Devine, 1989; Ge et al., 2009). Due to the negative side-effects of such an in-group bias, previous studies made huge efforts to develop new strategies to reduce the in-ethnicity bias (Hall & Crisp, 2005; Kurzban, Tooby, & Cosmides, 2001; Voorspoels, Bartlema, & Vanpaemel, 2014). For instance, a few studies pronounced the reduction of the in-ethnicity bias by developing a novel in-group bias based on the categorization of the membership in a mixed-ethnicity team, named in-team bias (Van Bavel, Packer, & Cunningham, 2008; Voorspoels et al., 2014). However, there is no evidence to support such an idea with the cultural neuroscience approach. Thus, it is currently unknown whether there are cultural differences in the neural basis of such a bias reduction.

Therefore, study two of the present dissertation applying the macroscopic perspective with a cultural neuroscience approach was designed mainly to focus on a) exploring cultural differences in social categorization based on the social coalitions of ethnicity and group memberships; b) examining the cultural differences in in-ethnicity bias reduction by developing a novel in-team bias. In addition, as mentioned, the social learning effect probably works on individuals' core culture values, which may lead to the changes of perceiving people from other cultures. Thus, two cultural groups were recruited in Germany: Chinese and German, resulting in the possibility to test the social learning effect on neural correlates of different in-group biases and on the in-ethnicity bias reduction by establishing the novel in-team bias in the Chinese group.

3.1 The effect of ethnicity and team-membership on face processing: A cultural neuroscience perspective[3]

3.1.1 Abstract

In-ethnicity bias, as one of the in-group biases, is widespread in different cultures, interfering with cross-ethnicity communication. Recent studies have revealed that an in-ethnicity bias can be reduced by an in-team bias caused by the membership in a mixed-ethnicity team. However, the neural correlates of different in-group biases are still not clear, especially regarding possible cultural differences. Forty-four participants (twenty Chinese and twenty-four Germans) were recruited and completed a social categorization fMRI-task, categorizing faces according to their ethnicity and learned team membership. Our behavioral results revealed both in-ethnicity and in-team bias in German participants, but not in Chinese participants. Our imaging results, however, showed both biases across all participants, as reflected in increased dorsal medial frontal cortex (MFC) activation for in-ethnicity, as well as in-team categorizations, while activation in ventral MFC was higher for in-ethnicity faces in Chinese participants than in the German participants. Our results highlight the importance of the dorsal MFC for in-group categorization across cultures and suggest that cultures might modulate in-group biases.

[3] Published paper: Yan, Z., Schmidt, S. N.L., Saur, S., Kirsch, P., & Mier, D. (in press). The effect of ethnicity and team-membership on face processing: A cultural neuroscience perspective. *Social Cognitive and Affective Neuroscience*.

3.1.2 Introduction

People categorize the social world into “us” and “them” for adaptation to the environment (Caporael, 1997), resulting in the so-called in-group bias reflected in perception, attitudes, and behaviors (Molenberghs & Louis, 2018). In-ethnicity, or so-called in-race bias, is one of the most prevalent in-group biases. It has been consistently found in different cultures (Han et al., 2013), and may lead to racial prejudice and stereotypes (Devine, 1989; Ge et al., 2009). Previous studies proposed that the in-ethnicity bias can be reduced by a novel in-group bias derived from the membership in a mixed-ethnicity team, so-called in-team bias (Van Bavel & Cunningham, 2009; Voorspoels et al., 2014). However, this reduction effect of in-ethnicity bias has been shown to be stronger in western relative to eastern culture (Ng, Steele, & Sasaki, 2016). Further, although a few of recent studies have initiated to explore the neural patterns of in-group biases (Shen, Hu, Fan, Wang, & Wang, 2018; Sheng & Han, 2012), the direct comparison of such neural patterns between cultures within one study is still missing.

The difference between individualistic and collectivistic value systems has been regarded as one of the most popular and significant cultural differences between western and eastern cultures (F. Li & Aksoy, 2007). Individualism is prominent in western countries and encourages an independent-self that is rather independent of social contexts and of others. In contrast, collectivism emphasizes fundamental social connections, resulting in an interdependent view of self, with high prevalence in East Asia (Markus & Kitayama, 2010). Differences in self-construal between individualism and collectivism probably lead to differences in perception and interaction with in- and out-group members (Cheon et al., 2011; Han, 2018). In the present study, we recruited two groups of participants which are from typical individualistic (Germans) and collectivistic (Chinese) culture, investigating possible cultural differences in neural correlates of the perception of in- and out-group members.

In-ethnicity bias, as one of the in-group biases, refers to the phenomenon that people are better and faster at recognizing people from their own-ethnicity compared to other ethnicities (Ge et al., 2009; Malpass & Kravitz, 1969). Due to in-depth encoding of in-ethnicity faces (Ratner, Dotsch, Wigboldus, van Knippenberg, & Amodio, 2014; Sporer, 2001), the in-ethnicity bias can also be presented in a seemingly paradoxical pattern

during categorization processes: People are faster to categorize a face from another-ethnicity than from one's own. This phenomenon is called other-ethnicity categorization advantage which is consistently found across cultures (Ge et al., 2009; Zhao & Bentin, 2011). Thus, we expected to find an other-ethnicity categorization advantage in both cultural groups.

However, as a byproduct of categorization regarding social coalitions, the in-ethnicity bias is not inevitable, but rather can be reduced when social coalitions change (Kurzban et al., 2001). Growing evidence suggests that the in-ethnicity bias can be reduced by a novel in-group bias (e.g. by a minimal group effect), caused by the membership in a mixed-ethnicity team, named in-team bias (Van Bavel & Cunningham, 2009; Voorspoels et al., 2014). It is assumed that the in-team bias is central to the phenomenon that people show greater resource allocation towards in-team members, once they were assigned to a (arbitrary and novel) team (Ratner & Amodio, 2013; Tajfel, Billig, Bundy, & Flament, 1971). Previous findings suggest that people from individualistic countries define social coalitions by rather broad social collectives, whereas people from individualistic countries define social coalitions by interpersonal relationships, demanding personal ties to include someone as an in-team member (Brewer and Yuki, 2007). This might suggest that an in-team bias is easier established in people from individualistic than in people from collectivistic countries (Ng et al., 2016; Snibbe, Kitayama, Markus, & SuZuki, 2003). However, recent cultural neuroscience studies with collectivistic samples also showed neural markers of a reduction of the in-ethnicity bias in empathy by manipulating the membership in a mixed-ethnicity group (Shen et al., 2018; Sheng & Han, 2012). Thus, we assumed to find an in-team bias in Germans on the behavioral level and examined if and how the reduction of an in-ethnicity bias differs between cultures.

The formation of an in-group bias (including in-ethnicity and in-team biases) has been recently considered a consequence of a dynamically interactive process of bottom-up processing and top-down expectations and motives of perceivers (Freeman & Ambady, 2011; Teufel & Nanay, 2017). This interactive process has been demonstrated in functional imaging studies across cultures. It is assumed that the amygdala response to faces from distinct social groups represents the bottom-up perceptual visual inputs (Rule et al., 2009; Van Bavel et al., 2008), while enhanced

fusiform gyrus (FFG) and medial frontal cortex (MFC) activation might indicate a top-down deeper process during in-group categorization (Feng et al., 2011; Gamond, Vilarem, Safra, Conty, & Grèzes, 2017; Van Bavel, Packer, & Cunningham, 2011). Increasing evidence suggests that enhanced activation in FFG and MFC seems to be consistently linked to the response to in-group members (Feng et al., 2011; Gamond et al., 2017; Van Bavel et al., 2011). In contrast, the amygdala's sensitivity to in- and out-group categorization is more complex and flexible, depending on the context/social goals (Molenberghs, 2013). Previous studies found elevated amygdala activation for processing out-ethnicity members when the social coalition (or in other words the group defining feature) was ethnicity (Firat, Hitlin, Magnotta, & Tranel, 2017; Sankar, Costafreda, Marangell, & Fu, 2018), but for processing in-team members when the social coalition switched to team memberships (Rule et al., 2009; Van Bavel et al., 2008). Thus, we expected to reveal increased amygdala activation for out-ethnicity and in-team categorization, and increased activation in FFG and MFC for categorizing in-ethnicity and in-team faces. Further, we assumed to observe an over-writing effect of the in-team bias on the in-ethnicity bias.

Besides, while the in-ethnicity bias has been developed since early childhood (Kinzler & Spelke, 2011), referring to a more profound and implicit type of in-group bias (Rule & Sutherland, 2017), the in-team bias is relatively novel and explicit as its formation happened within a short time period. This might indicate that the in-team bias requires more explicit, top-down and deeper processing relative to the in-ethnicity bias (Kawakami, Amodio, & Hugenberg, 2017; Mattan, Wei, Cloutier, & Kubota, 2018), which probably reflect in the FFG and MFC activation. However, due to the absence of direct empirical evidence, the neural differences between in-ethnicity and in-team bias are still unclear (Mattan et al., 2018; Rule & Sutherland, 2017). In the present study, we directly compared the neural correlates of in-ethnicity and in-team categorization in one paradigm and hypothesized increased activation in FFG and MFC for the in-team relative to in-ethnicity categorization.

A way to investigate the strength of implicit associations is the so-called implicit association task (IAT). Based on the notion that stronger associations cause longer reaction times (RTs) and require more cognitive control during the incongruent than congruent pairings (Greenwald, McGhee, & Schwartz, 1998), the extent of automatic

associations of in-ethnicity and in-team members can be easily investigated. Previous studies revealed that, by comparing the incongruent and congruent pairings, higher activation in the dorsolateral prefrontal cortex (DLPFC) and posterior parietal cortex (PPC) are apparent indicators of stronger implicit associations (Fedorenko, Duncan, & Kanwisher, 2013; Yan, Witthöft, Bailer, Diener, & Mier, 2017). However, to our knowledge, this approach has not been used to investigate differences in strength of associations in the in-ethnicity versus in-team bias. We assumed that the in-ethnicity bias is more implicit than the in-team bias and expected to observe increased activation in the DLPFC and PPC for categorizing in-ethnicity compared to in-team faces when categorized incongruently.

Prior studies suggest the in-ethnicity bias can be reduced by an in-team bias derived from a novel membership in a mixed-ethnicity group. This reduction effect on in-ethnicity bias, however, is probably modulated by culture, and its corresponding neural differences are still unknown. For exploring the cultural differences, we recruited two cultural groups of participants who are typical for collectivistic (China) and individualistic (German) countries. Referring to the minimal group paradigm (Tajfel et al., 1971), the present cultural neuroscience study created a novel in-team membership for each participant by arbitrary assigning them to a mixed-ethnicity team. We applied the social-categorization task with ethnicity-based and team-based categorizations with congruent and incongruent pairings respectively. In the congruent session, regarding behavior, we expected to find the in-ethnicity bias in both groups (Ge et al., 2009; Zhao & Bentin, 2011), and the in-team bias in the German group (Ng et al., 2016). Regarding brain activation, we hypothesized to observe increased amygdala activation for out-ethnicity relative to in-ethnicity faces (Firat et al., 2017; Sankar et al., 2018) and for in-team relative to out-team faces (Van Bavel et al., 2008). Further, we assumed to find higher activation in FFG and MFC for in-ethnicity than out-ethnicity faces and for in-team than out-team faces across participants (Feng et al., 2011; Van Bavel et al., 2011). Moreover, we attempted to explore the neural differences between in-ethnicity and in-team bias, assuming higher activation in the MFC and FFG for in-team versus in-ethnicity categorization across participants. Further, to explore the possible influence of exposure to the opposite culture on facial perception of other-cultural faces (Derntl, Habel, et al., 2009; Derntl et al., 2012), we recorded the duration of stay in Germany of our Chinese participants. In addition,

regarding the comparison between incongruent and congruent sessions, we hypothesized RTs are longer in the incongruent than in the congruent session across participants. On the neural level, we hypothesized to observe that categorizing the in-ethnicity and in-team faces in the incongruent session would result in higher activation of the DLPFC and PPC than in the congruent session across participants. Further, we assumed that Germans would show higher activation in the DLPFC and PPC than Chinese for categorizing the in-team faces in the incongruent versus congruent session.

3.1.3 Methods

3.1.3.1 Participants

Forty-nine healthy participants (twenty-four Chinese and twenty-five Germans) who met MRI inclusion criteria and had at least obtained a secondary school certificate were recruited and scanned in the Central Institute of Mental Health, Mannheim, Germany. Five of them were excluded, one due to brain abnormalities, and four due to response accuracy around chance (< 60% correct) during team-based categorization in the congruent session. Finally, forty-four participants (twenty Chinese (nine females, M_{age} = 26.02 ± 2.82) and twenty-four Germans (twelve females, M_{age} = 25.38 ± 5.44)) were included for data analyses. All participants were right-handed and had normal or corrected-to-normal vision. Groups were matched for age and gender. The study was approved by the local ethics board of the Medical Faculty Mannheim, University of Heidelberg. Before participation, participants were well-briefed about the procedures and purposes of the study and provided their written informed consent. All participants completed a digit span forward task, the social categorization fMRI-task and a series of questionnaires assessing clinical and cultural characteristics as well as personality traits (see Supplementary Text 1). All tasks and questionnaires were presented in participants' native language.

3.1.3.2 Procedure and Experimental Design

After the telephone screening, participants completed a series of online questionnaires. In the lab, participants were informed that they had been assigned to one team (team blue, or team red), followed by a learning procedure which consisted of two learning sessions and one test session (details of the learning procedure are provided in Supplementary Text 2 and Supplementary Table 2). Participants had to keep learning until they achieved 85% accuracy during the test session. The number of times that each participant completed the test session was recorded. Afterwards, participants had to learn the team memberships (team green, or team magenta) of geometric figures (triangles and circles), which were used for the control condition. Here, teams consisted of single geometric figures rather than of mixed geometric figures. For instance, all triangles belonged to team green, correspondingly, all circles

to team magenta. For counterbalancing the possible effect of the names of the team, we equally assigned our participants to each team name.

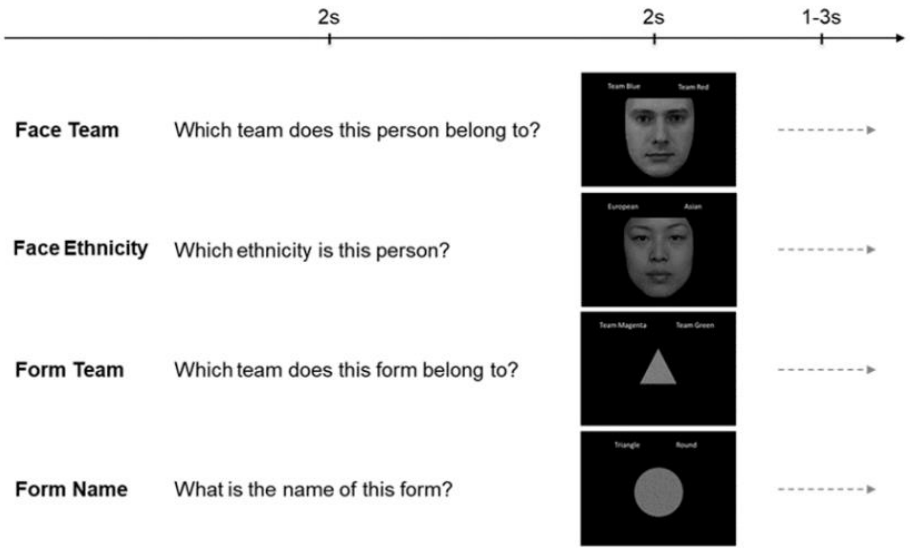


Figure 1 Social categorization task.

The social categorization fMRI-task consisted of two sessions, namely the congruent and incongruent session. Each session had four task conditions, presented in blocks: face-team, face-ethnicity, form-team, and form-name. Each condition started with an instruction, followed by six pictures consecutively. Participants needed to categorize the picture to the corresponding group, based on the prior instruction. For example, in the congruent face-team condition, participants first saw a sentence on the screen ("which team does this person belong to?"), and then they had to categorize the following six pictures according to the team affiliations that they learned in the learning procedure. In the incongruent session, however, participants had to give the reversed response in each task condition. That means, participants saw the same instruction as in the congruent session, for example in the face-team condition "which team does this person belong to?" but categorized the following faces to the affiliation which is opposite to the team that they learned in the learning procedure. The emotionally neutral facial stimuli used for the present study were selected from the Karolinska Directed Emotional Faces set for Caucasian stimuli (Goeleven et al., 2008) and from the Chinese Affective Picture System for Asian stimuli (Gong, Huang, Wang, & Luo, 2011). All stimuli were calibrated in luminance and contrast. We selected only face region of all stimulus persons to assure categorizations based on facial features. The duration of each session was 16 minutes, in total of 32 minutes for the whole task

(details of timing and presentation are presented in Figure 1 and Supplementary Text 3).

After scanning, participants were required to complete several additional questionnaires including a manipulation check questionnaire (details are presented in Supplementary Text 4). The results of all questionnaires are presented in Supplementary Table 1.

3.1.3.3 Data acquisition

FMRI data were acquired with a 3 Tesla Siemens Tim TRIO whole-body magnetic resonance tomograph (Siemens Medical Systems, Erlangen, Germany; acquisition protocol is provided in Supplementary Text 5).

3.1.3.4 Data Analyses

Behavioral data were analyzed with SPSS version 23. Due to the experimental design with three within-subject variables (congruency, category and affiliation) and one between-subject variable (group), 2 (congruency: congruency, incongruency) x 2 (category: team, ethnicity) x 2 (affiliation: in, out) x 2 (groups: Chinese and Germans) repeated measures ANOVAs were applied to investigate the differences in task performance between groups. Post-hoc tests were achieved with paired-sample t-tests. Pearson correlation was used to explore the associations between task performance and duration of stay in Germany in Chinese participants.

FMRI data analyses were conducted with statistical parametric mapping 12 (SPM12 version 6906). For preprocessing, the functional images were slice-time corrected to the middle (16th) slice, realigned to the first image of the run, then co-registered with the segmented anatomical scan, normalized to the MNI template with a 3 x 3 x 3 mm^3 resolution, and finally smoothed with a 9 mm full-width half-maximum kernel.

For the first level analysis, general linear models were applied for both congruent and incongruent sessions, each with twelve experimental conditions as regressors,

independent of accuracy of the participants' response: four for team-based categorization (in-team with Asian faces, out-team with Asian faces, in-team with European faces, out-team with European faces), four for ethnicity-based categorization (Asian faces in in-team members, Asian faces in out-team members, European faces in in-team members, European faces in out-team members), four for control condition (team-based categorization for circles and triangles, name-based categorization for circles and triangles), an additional one for the instruction period prior to each block, and the six movement regressors derived from the realignment procedure. Linear regression, modelling the hemodynamic response function, was performed at each voxel, using generalized least squares with a global approximate AR (1) autocorrelation model, and the time series was high-pass filtered using a 256 Hz function. Based on the model, contrasts of interest were calculated for the congruent and incongruent session respectively. The contrasts were: Faces > Forms as manipulation check; in_ethnicity > out_ethnicity based on the ethnicity categorization to investigate the in-ethnicity bias; in_team > out_team based on the team-based categorization to reveal the in-team bias; in_team > in_ethnicity to explore the neural differences between in-ethnicity and in-team bias. Moreover, we also built corresponding interaction contrasts to explore the neural correlates of implicit associations of the in-ethnicity bias: [(incongruent in_ethnicity > congruent in_ethnicity) > (incongruent out_ethnicity > congruent out_ethnicity)], of the in-team bias: [(incongruent in_team > congruent in_team) > (incongruent out_team > congruent out_team)], and of the differences in the in-ethnicity and in-team bias: [(incongruent in_team > congruent in_team) > (incongruent in_ethnicity > congruent in_ethnicity)].

For second-level analyses using random-effects models with ordinary least squares approach, we first applied one-sample t-tests to check the basic activation pattern of faces versus forms as a manipulation check. For investigating our hypotheses, we considered the number of runs during the test session as a covariate for controlling the effect of familiarity with stimuli. We used one-sample t-tests to investigate the neural correlates of in-ethnicity bias, in-team bias, the difference between in-ethnicity and in-team bias, and between out-ethnicity and out-team bias in the congruent session, as well as the difference in brain activation for in- and out-ethnicity bias, and in- and out-team bias between the congruent and incongruent sessions (i.e. interaction effect); the neural differences in these comparisons between groups were analyzed with

independent two-sample t-tests. The significance threshold for whole brain analyses was set to voxel-wise $p < 0.05$ *FWE-corrected*, $k \geq 10$. In addition, we applied region of interest (ROI) analyses according to our hypotheses with the masks of amygdala (for the contrasts out-ethnicity > in-ethnicity, and in-team > out-team), FFG and MFC (both for in-ethnicity > out-ethnicity, and for in-team > out-team; as well as for in-team > in-ethnicity) to the analyses in the congruent session; and with the masks of DLPFC (BA9 and BA46) and PPC (BA7 and BA40) to the interaction analyses. All masks were anatomical masks taken from the WFU pickatlas. The significance threshold for ROI analyses was set to voxel-wise $p < 0.05$ *small volume correction (svc),* $k \geq 10$. For investigating whether the neural correlates of our interest contrasts vary with duration of exposure to the opposite culture, we first extracted the first eigenvariate of each ROI from each contrast in the congruent session and from the interaction between incongruent and congruent sessions for each Chinese participants (no significance threshold was applied for eigenvariate extraction). Then Pearson correlations were applied to reveal associations between each extracted ROI signal and duration of stay in Germany in Chinese participants, using SPSS version 23.

3.1.4 Results

3.1.4.1 Self-Construal Scale and Task Manipulation Check

Based on the manipulation check questionnaire, all participants remembered their team affiliation after scanning. German participants reported higher sense of affiliation to the novel team, whereas Chinese participants showed better self-reported knowledge of team affiliation of the face stimuli at the end of the experiment (see Supplementary Text 4).

3.1.4.2 Behavioral Results

Chinese participants reported higher scores on vertical collectivism than German participants, whereas the German group showed higher scores on horizontal collectivism than the Chinese group. No other significant group differences were found in Self-Construal Scale (see Supplementary Table 1). Regarding task behavior, our results showed higher accuracy and shorter RTs of categorizations in the congruent session than in the incongruent session. In the congruent session, the other-ethnicity categorization advantage and the in-team bias were found in German but not in Chinese participants. During the team-based categorization, in-ethnicity faces were categorized faster than out-ethnicity faces across participants (see Supplementary Text 6 and Supplementary Table 3 and 4). In addition, task performance did not vary with the duration of stay in Germany in Chinese participants.

3.1.4.3 Imaging Results

3.1.4.3.1 Manipulation Check

Enhanced activation in the fusiform face area and occipital face area was found for face relative to form processing across participants and sessions, indicating the paradigm worked well and can differentiate faces and forms (see Supplementary Table 5 and Supplementary Figure 5).

3.1.4.3.2 Neural Correlates of the In-Ethnicity Bias and Its Cultural Differences

In the congruent session, ROI-analyses revealed increased activation in right dorsal MFC for in- versus out-ethnicity categorization. Regarding group differences, Chinese, compared to Germans, showed higher activation in the left occipital lobe for categorizing in-ethnicity than out-ethnicity faces with whole brain analyses (see Figure 3), whereas Germans showed higher activation in the right occipital lobe in comparison to Chinese (see Figure 3). ROI analyses revealed that Chinese showed higher activation in the right ventral MFC for categorizing in- versus out-ethnicity faces than Germans (see Figure 2 and Supplementary Table 6).

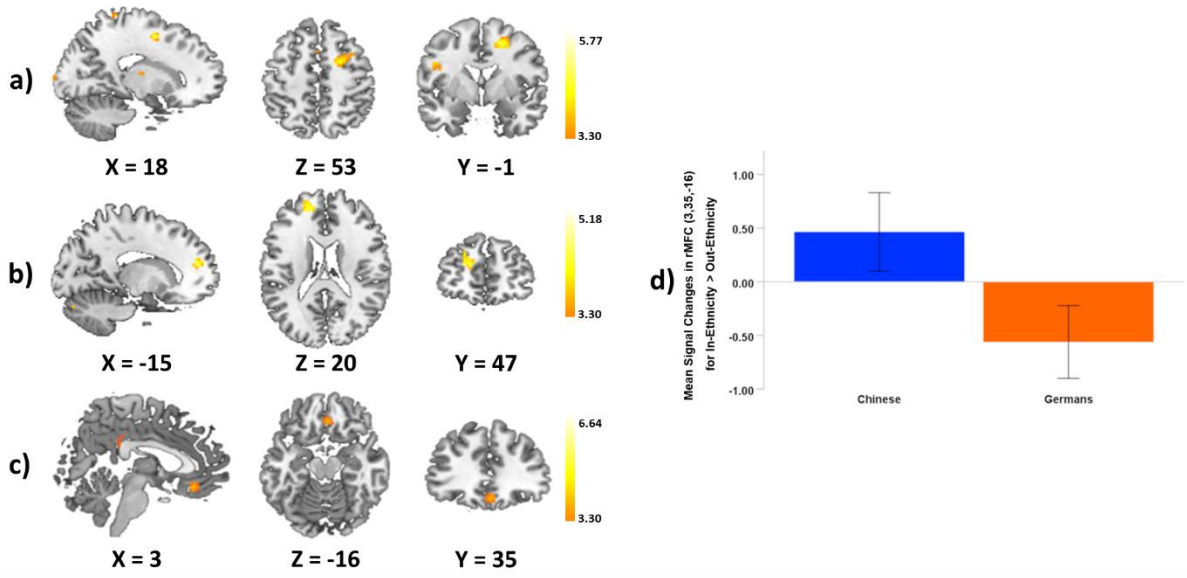


Figure 2: Neural correlates of ethnicity and team categorization. a) Increased activation in the posterior medial frontal cortex for categorizing faces from their own ethnicity compared to those from another ethnicity. b) Increased activation in the medial prefrontal cortex for categorizing the faces from the own team in comparison to those from the other team. c) and d) Higher activation in the medial frontal cortex for categorizing faces from categorizing faces from their own ethnicity compared to those from another ethnicity in Chinese than Germans. Note: threshold for displaying is voxel-wise $p < .001$ uncorrected, $k \geq 10$; rMFC indicates right medial frontal cortex.

When comparing the incongruent and congruent session, no significant results were found for categorizing the in- versus out-ethnicity faces across participants. However, our results revealed that the in-ethnicity faces, relative to the out-ethnicity faces, resulted in stronger activation in the left occipital lobe in Chinese than Germans, but in

the right occipital lobe in Germans than in Chinese (see Supplementary Table 6). No other significant results were found with this contrast.

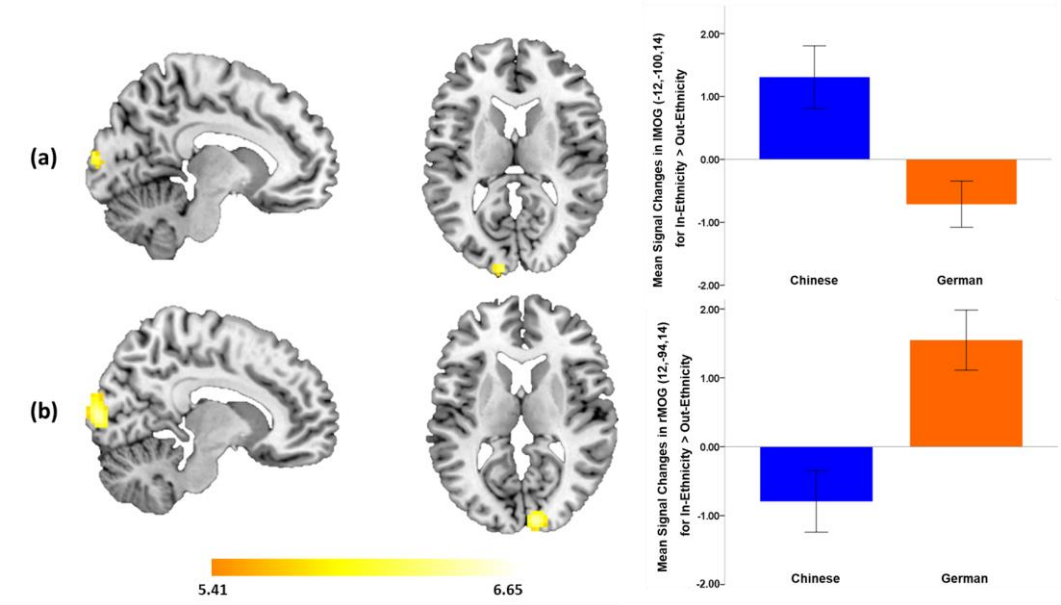


Figure 3 Neural correlates of cultural differences in the in-ethnicity bias. (a) In comparison to the German group, the Chinese group showed higher activation in the left middle occipital gyrus (MNI coordinates: -12,-100,14) for categorizing the in-ethnicity faces than out-ethnicity faces. (b) In comparison to the Chinese group, the German group showed higher activation in the right middle occipital gyrus (MNI coordinates: 12,-94,14) for categorizing the in-ethnicity faces than out-ethnicity faces. Note: lMOG means left middle occipital gyrus and rMOG means right middle occipital gyrus; significance threshold was voxel-wise $p < 0.05$, *FWE-corrected,* $k \geq 10$.

3.1.4.3.3 Neural Correlates of the In-Team Bias and Its Cultural Differences

In the congruent session, we found enhanced activation in the left dorsal MFC for categorizing in- relative to out-team faces across participants with ROI-analyses. No significant group differences were found with this contrast (see Supplementary Table 7).

No significant activation differences were found for categorizing the in- versus out-team faces when comparing the incongruent and congruent session, neither across participants nor between groups.

3.1.4.3.4 Neural Differences between the In-ethnicity Bias and In-team Bias

In the congruent session, for in-ethnicity versus in-team categorizations, whole brain analyses revealed increased activation in regions of default mode network including posterior cingulate cortex and medial prefrontal cortex, and middle temporal gyrus across participants (see Supplementary Figure 6(a) and Supplementary Table 8), whereas enhanced activation was found for categorizing in-team versus in-ethnicity faces mainly in regions of frontal (including insula), parietal and occipital lobe (see Supplementary Figure 6(b) and Supplementary Table 9). ROI analyses showed enhanced activation in bilateral amygdala for categorizing in-ethnicity relative to in-team faces across participants (see Supplementary Table 8), whereas higher activation in bilateral FFG and MFC was found for categorizing in-team relative to in-ethnicity faces (see Supplementary Table 9).

We found a comparable pattern for out-team versus out-ethnicity, as for in-team versus in-ethnicity. These results are presented in the supplement (see Supplementary Figure 7, Supplementary Table 10 and 11). Since these results suggest that team categorizations were more difficult than ethnicity categorizations, independent of the in- or out-group status, further corresponding comparisons between the congruent and incongruent session and between groups would not reveal specific insight into overcoming the in-ethnicity bias, and thus are not presented.

3.1.5 Discussion

The present study aimed at investigating cultural differences in in-ethnicity and in-team bias and how in-ethnicity bias can be reduced by the in-team bias. Behaviorally, we found the in-ethnicity and in-team bias only in Germans. Our neural results highlight the importance of the MFC activation in group categorization and reflect neural differences in the in-ethnicity bias between groups. In addition, our results suggest that the in-ethnicity bias is not easily over-written by the in-team bias across groups.

We found the in-ethnicity bias only in Germans but not in Chinese, which is inconsistent with prior studies showing an in-ethnicity bias in both cultures (Zhao & Bentin, 2008, 2011). Besides, we did not reveal differences in core cultural values between groups. These findings might attribute to the recruitment of Chinese participants who have lived in Germany. With increasing frequency of contacting people from the opposite culture, the in-ethnicity bias and their collectivistic cultural values might be weakened (Chance, Goldstein, & McBride, 1975). In line with previous studies (Feng et al., 2011), we found increased activation in dorsolateral MFC for in- versus out-ethnicity categorization across participants. The activation occurred in a dorsal part of the MFC that is known to be associated with memory (Euston, Gruber, & McNaughton, 2012) and self-identity processes (D'Argembeau et al., 2007; Jenkins & Mitchell, 2011). Increased dorsal MFC activation for in-ethnicity faces may reflect an increase in self-related processing, demonstrating a close association of the participants with people from their own culture.

Compared to Germans, Chinese showed higher ventral MFC activation for in- versus out-ethnicity categorization. As the ventral MFC is linked to represent the preference of stimuli (Van Bavel et al., 2008), even if the task did not require subjects to explicitly think of the extent of preference of the stimuli (Levy, Lazzaro, Rutledge, & Glimcher, 2011). Thus, our finding might be interpreted as higher preference of in-ethnicity members in Chinese. However, this neural pattern of higher preference for in-ethnicity members was not reflected in behavior.

Interestingly, for in- versus out-ethnicity categorizations, we found higher activation in the left visual cortex in Chinese than Germans, but higher activation in the right visual cortex in Germans than Chinese. Prior cross-cultural studies suggested that in-

ethnicity faces are processed via holistic information across cultures, whereas feature-detection processing was used for out-ethnicity faces (Ge et al., 2009; Zhao & Bentin, 2011). Our results regarding German participants are consistent with previous findings of studies with individualistic samples that holistic processing relies more on the right hemisphere and the feature-detection processing on the left hemisphere (Rossion et al., 2003; Rossion et al., 2000). However, based on our knowledge, only one fMRI study has focused on the categorization of in-ethnicity faces with a collectivistic sample (Feng et al., 2011), and their findings are consistent with ours, discovering higher left visual cortex activation for in- versus out- ethnicity categorization in Chinese. It may imply a different hemisphere functioning for holistic and feature-detection processing during face perception between cultures. Importantly, with reversing responses to categorize faces based on ethnicity during the incongruent condition, the neural patterns have also presented in a reversed way when we compared the in- versus out-ethnicity categorization in incongruent versus congruent pairings. These findings might represent the capacity of brain of flexibly switching processing modes for in- and out-ethnicity faces, according to the focus of in- versus outgroup, and may suggest differences in processing of faces of the own ethnicity between cultures. However, the result might also be the effect of less differences in brain activation between incongruent and congruent pairings in one of the groups. Thus, it should be kept in mind that these are complex interactions which need replication and should be interpreted with caution.

Consistent with our hypothesis, our results show an in-team bias in Germans (Van Bavel et al., 2008; Voorspoels et al., 2014), but not in Chinese (Ng et al., 2016). As we mentioned, people from individualism interpret social groups as broad social collectives, implying that they treat strangers who share the group membership with them as “in-group” members (Brewer & Yuki, 2007). In contrast, people with a collectivistic background consider the social network as interpersonal relationships, demanding personal ties to include others as in-group member (Brewer & Yuki, 2007). The team membership in the present study was established without pre-existing personal ties and contact. Thus, it seems harder for Chinese than for Germans to develop the in-team bias.

However, we observed the in-team bias across all participants on the neural level. In line with prior findings (Gamond et al., 2017; Molenberghs & Morrison, 2014), we found higher dorsal MFC activation for categorizing in-team versus out-team faces across cultures. As mentioned, dorsal MFC activation has been associated with self-referential processing (D'Argembeau et al., 2007; Molenberghs & Morrison, 2014). Our results may reflect an increase in self-related brain activation towards in-team than out-team members. Moreover, no significant neural differences in processing in-team faces were found between cultures, probably suggesting a common neural code for processing in-team members across cultures. In short, combined with the finding of in-ethnicity bias, we suggest that dorsal MFC represents a core brain area for in-group categorization independent of social coalitions (i.e. based on ethnicity and on team membership).

In line with previous findings (Van Bavel et al., 2008), we found that RTs were around 300ms faster in in-ethnicity than in-team categorization, suggesting that in-ethnicity categorization is easier than the latter. In addition, the RTs were faster in in-ethnicity than out-ethnicity categorization during the team-based categorization reflecting an in-ethnicity bias rather than other-ethnicity categorization advantage. These findings demonstrate that the team-based categorization probably requires additional memory retrieval than the ethnicity-based categorization, which may reflect the former representing higher-order processing (e.g. face recognition). This seems plausible when considering that team members were learned directly before the experiment, whereas the connection with own-ethnicity members developed since early childhood (Kinzler & Spelke, 2011). Our fMRI results mostly point to differences in the cognitive demands of the categorization tasks. We found enhanced activation in regions of default mode network and amygdala for in-ethnicity versus in-team, and out-ethnicity versus out-team categorization across groups. The activation in the default mode network is associated with resting states and internally focused self-referential tasks (Buckner, Andrews‐Hanna, & Schacter, 2008). The amygdala is a typical region for detecting salience in a bottom-up manner (Van Bavel et al., 2008). Such findings suggest that compared to the team-based categorizations, ethnicity-based categorizations require less attentional control and rely largely on bottom-up visual attention.

By contrast, we observed increased activation in the anterior insula, MFC, and FFG for the categorization of the in-team versus in-ethnicity, and of out-team versus out-ethnicity faces. Like the amygdala, the activation of anterior insula is associated with salience detection (Rilling, Dagenais, Goldsmith, Glenn, & Pagnoni, 2008), but the anterior insula also seems to be involved in high-level cognitive control processes (Menon & Uddin, 2010). In addition, the dorsal MFC is not only associated with self-referential processing (D'Argembeau et al., 2007), but also with action monitoring and attention during social cognition (Amodio & Frith, 2006), and enhanced FFG activation for processing in-team faces has been interpreted as the in-depth encoding of faces (Van Bavel et al., 2011). Together, consistent with our assumption, the in-team categorization might require more top-down attentional control than the in-ethnicity categorization (Mattan et al., 2018). However, since we found a comparable activation pattern for out-team versus out-ethnicity judgments, we cannot draw specific conclusions about the processing of different in-groups but can only conclude about team versus ethnicity processing in general. In consequence, we omitted planned comparisons of in-team versus in-ethnicity comparisons between the congruent and incongruent session, as well as the corresponding group comparisons, because they would reflect interactions based on differences in task difficulty, but not specifically of over-writing in-ethnicity bias.

While we recruited participants who were socialized in two different cultures: Collectivism and Individualism, our work did not reveal an in-ethnicity bias in Chinese behaviorally and we also did not discover the expected differences in the core cultural values between the two groups (see supplementary text 1). These findings may be attributed to the recruitment of both groups in Germany. As exposure to the opposite culture may alter the cultural representation (such as self-construal (Yamada & Singelis, 1999)), the cultural values in our Chinese group may have been altered towards the German group since they arrived in Germany. Besides, cultural identity in people studying or living in other cultures might be prone to that culture, even before leaving for there. This might also explain why we found no associations between task performance and duration of stay. Thus, it is necessary for future studies to establish the cultural groups by recruiting participants living in their own culture. Further, future studies might refer to questionnaires that are more sensitive to the cultural background of the participants, in addition to assessing their current cultural values. Interestingly,

German participants reported higher sense of affiliation to the novel team, whereas Chinese participants showed better self-reported knowledge of team affiliation of the face stimuli after the fMRI session. It seems that better self-reported knowledge of team affiliation of the face stimuli did not increase the sense of affiliation to the novel team in the Chinese group. Our behavioral, as well as our neural data, suggest that team and ethnicity categorizations may reflect distinct levels of processing with a more higher-order processing of team than ethnicity categorizations. Since we found a comparable pattern for in-group (in-ethnicity versus in-team), as for out-group (out-ethnicity versus out-team) comparisons, the minimal group approach (Brewer & Yuki, 2007) that we chose might not be optimal for investigating the neural bases of team versus ethnicity processing. Together these results suggest that future studies might use paradigms that are based on already existing ties, such as memberships in mixed sport-teams in which participants know their team-members before joining the study. In addition, our results of different hemispheric functions in the visual cortex between cultures while categorizing faces according to their ethnicity warrant replication.

With the cultural neuroscience approach, we revealed that the dorsal MFC may present a common neural code for in-group biases across cultures. In addition, our findings shed light on the cultural effect on in-ethnicity biases, suggesting ventral MFC and visual cortex as targets for a deeper understanding of differences in in-ethnicity biases between cultures. Our results also suggest that the in-ethnicity bias is not easily overcome by the in-team bias. Future studies should extend the present study by developing suitable experimental paradigms allowing the differentiation between different types of in-group biases to a) explore mechanisms of overcoming in-group bias and b) gain deeper knowledge on cultural differences in in-group biases.

3.1.6 Supplementary materials

3.1.6.1 Supplementary text

3.1.6.1.1 Supplementary Text 1 Questionnaires

To assess emotional processing, participants filled in the Difficulties in Emotion Regulation Scale [DERS (Gratz & Roemer, 2004); Chinese version (L. Wang, Liu, Li, & Du, 2007), German version (Ehring, Fischer, Schnülle, Bösterling, & Tuschen-Caffier, 2008)], as well as the emotion regulation questionnaire [ERQ (Gross & John, 2003); Chinese version (C. Zhang et al., 2014), German version (Abler & Kessler, 2009)]; to assess deficits in the identification and description of own feelings, they completed the Toronto-Alexithymia-Scale [TAS-20 (Bagby, Parker, & Taylor, 1994); Chinese version (Yi, 2003); German version (Bach, Bach, de Zwaan, & Serim, 1996)]. To assess further dimensions that are relevant to social processing, participants completed the social interaction anxiety scale [SIAS (Mattick & Clarke, 1998); Chinese version (Ye, Qian, Liu, & Xi, 2007), German version (Eidecker, Glöckner-Rist, & Gerlach, 2010)], the Beck Depression Inventory-II [BDI-II (Beck, Steer, & Brown, 1996); Chinese version (Lu, Che, Chang, & Shen, 2002), German version (Hautzinger, Keller, & Kühner, 2006)], the schizotypal personality questionnaire [SPQ (Raine, 1991); Chinese version (Yu, Bernardo, & Zaroff, 2016), German version (Klein, Andresen, & Jahn, 1997)], and the NEO-Five-Factor Inventory [NEO-FFI (Costa & McCrea, 1992); Chinese version (L. Zhang, 2006), German version (Borkenau & Ostendorf, 1993)]. To estimate the degree of endorsement of individualistic and collectivistic values, participants completed the Self-Construal Scale [SCS, (Triandis & Gelfand, 1998), which has been applied in one cross-cultural study with Chinese and German participants (de Greck et al., 2012)]. In addition, the digit-span task (Wechsler, 2014) was applied to get an estimate of intelligence. All questionnaires were provided in German and Chinese language.

3.1.6.1.2 Supplementary Text 2 Details of Learning and Test Session

In the learning sessions, participants first spent 5 minutes to learn the in- and out-team members through two sheets of paper, each presenting 12 faces of in- and out-team members, respectively. Both teams had equal counts of men/women and

Chinese/Caucasians. The facial stimuli with a neutral facial expression were selected from the Karolinska Directed Emotional Faces set for Caucasian stimuli (Goeleven et al., 2008) and from the Chinese Affective Picture System for Chinese stimuli (Gong et al., 2011). In the second learning session, faces were presented at a laptop one at a time in the middle of the screen for 5s with a colored background indicating the team affiliation of the face. Above the picture, the names of both teams (team red and team blue) were shown on each side of the screen. Participants needed to categorize each face into the corresponding team by pressing the left or right arrow on the keyboard. Each face was shown once during this learning session, resulting in a total of 24 trials. The test session came after the second learning session. Different from the second learning session, each facial stimulus was depicted with a standardized black background and was presented for 2 s. following each stimulus. Feedback informed the participants whether their response was correct, wrong, or too slow. Each face was shown three times during this session, resulting in a total of 72 trials. The accuracy of responses was presented at the end of the test session. Participants had to repeat the learning session two and the test session until they achieved 85% accuracy. If the participants did not reach 85% accuracy after three times, they were allowed to repeat the learning session one once again. The number of times that each participant completed the test sessions was recorded.

3.1.6.1.3 Supplementary Text 3 Experimental Paradigm

Each session contained eight runs of four blocks. Each block included six trials, for a total of 192 trials for each session, 384 trials in total for the whole task. The blocks were presented in the order face-team, face-ethnicity, form-team, and form-name. Six of the twenty-four facial pictures were randomly selected for each face-team and face-ethnicity condition, and six of the twenty-four pictures of geometric figures were randomly selected for each form-team and form-name. In the end, each of the forty-eight pictures (twenty-four faces and twenty-four figures) was presented and categorized four times (two by team categorization and two by ethnicity/name categorization). Each block started with presenting an instruction for 2 s, followed by a picture (a facial expression or a geometric figure) with the names of the two team affiliations above. Participants were required to categorize the picture to the corresponding affiliation in 2 s. Trials were separated by a fixation cross with a mean

duration of 2 s (with a jitter of 1-3 s, in pseudorandom order). The Inter-Trial-Interval mean amounted to 4 s (with a jitter of 3-5 s, in pseudorandom order). Thus, the social categorization task lasted approximately 16 minutes per session, resulting in a total of 32 minutes for the whole task. The task was implemented with Presentation software, version 9.50 (Neurobehavioral Systems Albany, CA, USA), and was presented on a monitor outside of the scanner. Participants could see the monitor through a mirror which was set up on the head coil. Participants responded using a four-button diamond response device (Current Designs, Inc., Philadelphia, PA).

3.1.6.1.4 Supplementary Text 4 Manipulation Check Questionnaire

Please write down the name of the team you belong to _____
How long have you been in Germany (only for Chinese)? _____
How often do you contact Chinese (only for German)? _____
How long did you stay in China (only for German)? _____
How many Chinese people do you know (only for German)? _____

Please read each question carefully and answer accordingly to your own feelings. Please mark the appropriate number after each statement. Note: 1 indicates "not at all"; 5 indicates "very much".

1	How much do you feel that you belong to your team?	1	2	3	4	5
2	How easy was it for you to learn the team affiliations of the faces?	1	2	3	4	5
3	How easy was it for you to learn the team affiliations of the geometric figures?	1	2	3	4	5
4	How well did you remember the team affiliations of the faces at the end of the experiment?	1	2	3	4	5
5	How well did you remember the team affiliations of the geometric figures at the end of the experiment?	1	2	3	4	5
6	How easy was it for you to invert the response to the ethnicity of the faces in the second session?	1	2	3	4	5
7	How easy was it for you to invert the response to the team affiliations of faces in the second session?	1	2	3	4	5
8	How easy was it for you to invert the response to the names of geometric figures in the second session?	1	2	3	4	5
9	How easy was it for you to invert the response to the team affiliations of geometric figures in the second session?	1	2	3	4	5

Results of the Manipulation Check Questionnaire

Nr.	Chinese (n = 20)		German (n = 24)		*t*	*p*	*d*
	Mean	SD	Mean	SD			
1	2.30	1.22	3.13	1.30	-2.16	0.037*	0.66
2	2.80	0.83	2.71	0.96	0.34	0.739	-0.10
3	4.90	0.31	4.75	0.85	0.75	0.457	-0.24
4	4.20	0.62	3.13	0.80	4.92	< 0.001***	-1.51
5	4.75	0.72	4.71	0.55	0.22	0.828	-0.07
6	4.30	0.80	4.33	0.82	-0.14	0.892	0.04

7	3.60	1.27	2.96	0.96	1.91	0.063	-0.57
8	4.65	0.67	4.46	0.88	0.80	0.430	-0.24
9	4.55	0.83	4.17	10.05	1.33	0.192	-0.41

Note: * < *0.05,* *** < *0.001*; Nr. 1-9 indicate the 1-9 items in the manipulation check questionnaire.

3.1.6.1.5 Supplementary Text 5 Imaging Data Acquisition

The study started with the functional scans, followed by an anatomical scan. Functional scans were obtained by using a T2*-weighted gradient echo planar imaging sequence (TR = 2000 ms; TE = 28 ms; flip angle 80 degree; matrix: 64 x 64 mm). Each volume consisted of 33 slices, acquired in a descending order with a slice-thickness of 3 mm with 1 mm gap (resulting voxel size: 3 x 3 x 4 mm3). Slices were aligned to anterior-posterior commissure and additionally flipped minus 25°. The whole brain was covered. Each session (congruent and incongruent) had 492 scans, with a total of 984 scans for the whole experiment. The first 4 scans of each session were discarded to account for saturation effects. After functional imaging, a T1-weighted anatomical scan (192 slices, 1 x 1 x 1 mm voxel size) was acquired.

3.1.6.1.6 Supplementary Text 6 Behavioral Results

3.1.6.1.6.1 Across all task sessions

Across all task sessions, 2 (congruency: congruency, incongruency) x 2 (category: team, ethnicity) x 2 (affiliation: in, out) x 2 (groups: Chinese and Germans) repeated measurements ANOVAs were applied to investigate the differences in task performance between groups.

In terms of accuracy, the repeated measures ANOVA revealed significant main effects of congruency ($F(1, 42) = 7.70$, $p = 0.008$, $\eta^2 = 0.16$) and category ($F(1, 42) = 243.67$, $p < 0.001$, $\eta^2 = 0.85$). No interactions were found on the accuracy. Post-hoc tests showed that the accuracy in the congruent condition is higher than in the incongruent condition ($t(43) = 2.85$, $p = 0.007$, $d = 0.43$); and the accuracy for ethnicity categorization is higher than for team categorization ($t(43) = 15.52$, $p < 0.001$, $d = 2.33$).

Regarding the reaction times, the repeated measures ANOVA found significant main effects of congruency (F (1, 42) = 44.48, $p < 0.001$, $\eta^2 = 0.51$) and category (F (1, 42) = 164.89, $p < 0.001$, $\eta^2 = 0.80$). Significant interactions were also found between category and affiliation (F (1, 42) = 8.89, $p = 0.005$, $\eta^2 = 0.18$), as well as among category, affiliation, and groups (F (1, 42) = 5.65, $p = 0.022$, $\eta^2 = 0.12$). Post-hoc tests revealed that the reaction times in the congruent condition are shorter than in the incongruent condition (t (43) = -6.75, $p < 0.001$, d = -1.02); the reaction times for ethnicity categorization are faster than for team categorization (t (43) = 12.86, $p < 0.001$, d = 1.94); the reaction times for in-team categorization are faster than for out-team categorization (t (43) = -2.82, $p = 0.007$, d = -0.40); the reaction times for in-ethnicity categorization are slower than for out-ethnicity categorization (t (43) = 2.05, $p = 0.046$, d = 0.31); the reaction times for in-ethnicity categorization are faster than for in-team categorization (t (43) = -10.53, $p < 0.001$, d = -1.59). In addition, post-hoc tests found that the German group categorized in-team members faster than out-team members (t (23) = -2.71, $p = 0.013$, d = -0.55), categorized the in-ethnicity members slower than out-ethnicity members (t (23) = 3.29, $p = 0.003$, d = 0.67), and categorized the in-ethnicity members faster than in-team members (t (23) = -7.44, $p < 0.001$, d = .1.52). Post-hoc tests also found that the Chinese group categorized in-ethnicity members faster than in-team members (t (19) = -7.31, $p < 0.001$, d = -1.64).

3.1.6.1.6.2 In the congruent condition

For comparing the results with previous findings (Van Bavel et al., 2008), we also did 2 (category: team, ethnicity) x 2 (affiliation: in, out) x 2 (stimuli: in_ethnicity/team, out_ethnicity/team) x 2 (groups: Chinese and Germans) repeated measures ANOVAs to investigate the differences in task performance (accuracy and reaction times) between groups only in the congruent session.

In terms of accuracy, the repeated measures ANOVA revealed significant main effects of congruency (F (1, 42) = 273.52, $p < 0.001$, $\eta^2 = 0.85$) and interactions between

category and stimuli (F (1, 42) =4.99, p = 0.031, η^2 = 0.11), as well as among affiliation, stimuli and groups (F (1, 42) = 4.18, p = 0.047, η^2 = 0.09). Post-hoc tests showed that the German group had higher accuracy for categorizing the in-ethnicity members than the in-team members (t (23) = 7.41, p < 0.001, d = 1.51), and for categorizing in-ethnicity members than out-ethnicity members from out-team members (t (23) = 3.87, p = 0.001, d = 0.79). Post-hoc tests also showed that the Chinese group had higher accuracy for categorizing the in-ethnicity members than in-team members (t (19) = 5.13, p < 0.001, d = 1.15).

Regarding the reaction times, the repeated measures ANOVA revealed significant main effects of congruency (F (1, 42) = 44.48, p < 0.001, η^2 = 0.51) and stimuli (F (1, 42) = 8.93, p = 0.005, η^2 = 0.18). Significant interactions were also found between stimuli and group (F (1, 42) = 12.14, p = 0.001, η^2 = 0.22), between category and affiliation (F (1, 42) = 9.83, p = 0.003, η^2 = 0.19), among category, affiliation, and group (F (1, 42) = 5.43, p = 0.025, η^2 = 0.11), as well as among category, stimuli, and group (F (1, 42) = 14.37, p < 0.001, η^2 = 0.26). Post-hoc tests revealed that the German group showed shorter RTs for categorizing out-ethnicity members than in-ethnicity members (t (23) = -3.51, p = 0.002, d = -0.72), for categorizing in-team members than out-team members (t (23) = -2.90, p = 0.002, d = -0.59), and for categorizing in-ethnicity members than in-team members (t (23) = -6.69, p < 0.001, d = -1.37), as well as for categorizing the in-ethnicity members than out-ethnicity members of in-team members (t (23) = -4.16, p < 0.001, d = -0.85), as well as of out-team members (t (23) = -5.02, p < 0.001, d = -1.03). Post-hoc tests also showed the Chinese group categorized in-ethnicity members faster than in-team members (t (19) = -5.55, p < 0.001, d = -1.24). The results of the group comparisons revealed that the German group, compared to the Chinese group, presented better accuracy for categorizing the in-ethnicity faces of out-team members (t (42) = 2.25, p = 0.030, d = 0.67); longer RTs for categorizing the out-ethnicity faces of in-team faces (t (42) = 2.63, p = 0.012, d = 0.78), and the out-ethnicity faces of out-team faces (t (42) = 3.74, p = 0.001, d = 1.14).

3.1.6.1.6.3 The over-writing effect in the congruent session

In the team-based categorization, paired sample t-tests revealed better accuracy for categorizing in- than out-ethnicity faces across all participants (t (43) = 2.45, p = 0.018,

d = 0.37, also see Supplementary Table 4 and Supplementary Figure 3). On the other hand, in the ethnicity-based categorization, no significant difference was revealed between in- and out-team categorization across all participants. In addition, no group differences were found in terms of accuracy on the over-writing effect (see Supplementary Table 4 and Supplementary Figure 3).

Regarding the reaction times, in the team-based categorization, all participants categorized in-ethnicity faces faster than out-ethnicity faces ($t(43) = -2.91$, $p = 0.006$, $d = 0.44$, also see Supplementary Table 4 and Supplementary Figure 4), but no significant difference was revealed between in-team and out-team categorization in the ethnicity-based categorization with paired sample t-tests. By comparing the groups, independent sample t-tests showed shorter reaction times in the Chinese group than in the German group while categorizing in- versus out-ethnicity faces during the team-based categorization (see Supplementary Table 4 and Supplementary Figure 4).

3.1.6.2 Supplementary tables

3.1.6.2.1 Supplementary Table 1 Group comparisons of scores on questionnaires

	Chinese (n = 20)		Germans (n = 24)		*t*	*p*	*d*
	Mean	*SD*	*Mean*	*SD*			
Beck Depression Inventory-II	8.05	5.37	6.50	6.63	0.84	0.405	-0.26
Difficulties in Emotion Regulation Scale	2.29	0.45	2.03	0.56	1.69	0.099	-0.52
Emotion Regulation Questionnaire	4.60	0.64	4.63	0.74	-0.12	0.906	0.04
Schizotypal Personality Questionnaire	23.50	9.95	14.58	11.12	2.78**	0.008	-0.85
Social Interaction Anxiety Scale	28.10	11.59	22.58	10.75	1.64	0.109	-0.49
Toronto Alexithymia Scale	50.25	8.53	43.21	11.55	2.26*	0.029	-0.69
Revised NEO Personality Inventory							
Neuroticism	1.79	0.55	1.63	0.76	0.81	0.421	-0.25
Extraversion	2.17	0.40	2.35	0.56	-1.20	0.235	0.37
Openness	2.35	0.42	2.58	0.62	-1.46	0.152	0.45
Agreeableness	2.67	0.28	2.77	0.57	-0.72	0.476	0.22
Conscientiousness	2.50	0.46	2.93	0.49	-2.97**	0.005	0.90
Self-construal Scale							
Individualism	61.70	9.04	61.04	9.72	0.23	0.819	-0.07
Horizontal Individualism	27.80	5.11	28.42	3.89	-0.46	0.652	0.14
Vertical Individualism	33.90	7.46	32.63	8.02	0.54	0.591	0.16
Collectivism	67.05	12.60	67.00	8.39	0.02	0.988	-0.01
Horizontal Collectivism	37.70	7.86	42.00	5.80	-2.09*	0.043	0.62
Vertical Collectivism	29.35	6.86	25.00	4.66	2.49*	0.017	0.74

Note: ** $p < 0.05$, **$p < 0.01$*

3.1.6.2.2 Supplementary Table 2 Group comparisons of performances in the test session.

	Chinese (n = 20)		Germans (n = 24)		*t*	*p*	*d*
	Mean	*SD*	*Mean*	*SD*			
Number of runs for test session (times)	4.15	1.09	4.38	1.76	-0.50	0.622	0.16
Accuracy in the last test session (%)	90.70	3.51	90.83	3.14	-0.13	0.895	0.04

3.1.6.2.3 Supplementary Table 3 Mean accuracies and reaction times in the categorization tasks and group comparisons.

	Whole Sample (n = 44)		Chinese (n = 20)		Germans (n = 24)		*t*	*p*	*d*
	Mean	*SD*	*Mean*	*SD*	*Mean*	*SD*			
Congruent Session (accuracy)									
In-team	82.32	8.81	81.99	9.38	82.61	8.50	-0.23	0.820	0.07
Out-team	81.67	9.01	81.33	10.11	81.96	8.20	-0.23	0.819	0.07
In-ethnicity	95.35	5.53	94.66	5.00	95.93	5.98	-0.75	0.455	0.23
Out-ethnicity	96.48	5.00	96.52	5.14	96.45	4.99	0.04	0.966	-0.01
Incongruent Session (accuracy)									
In-team	81.77	9.31	83.48	7.30	80.33	10.64	1.12	0.269	-0.35
Out-team	78.88	12.57	78.62	12.05	79.10	13.25	-0.13	0.900	0.04
In-ethnicity	93.66	7.73	92.88	8.51	94.30	7.14	-0.60	0.549	0.18
Out-ethnicity	92.67	9.00	91.76	10.06	93.42	8.15	-0.61	0.459	0.18
Congruent Session (reaction times)									
In-team	1218.30	108.23	1197.42	118.97	1235.69	97.53	-1.17	0.248	0.35
Out-team	1268.28	122.59	1225.95	108.59	1303.56	124.49	-2.18*	0.035	0.66
In-ethnicity	1049.93	110.85	1032.67	116.04	1064.31	106.64	-0.94	0.352	0.28
Out-ethnicity	1020.18	107.09	1042.01	84.82	1001.99	121.40	1.24	0.221	-0.38
Incongruent Session (reaction times)									
In-team	1319.57	124.34	1306.27	120.22	1330.65	129.16	-0.64	0.523	0.20
Out-team	1348.99	126.43	1322.13	134.68	1371.37	117.26	-1.30	0.202	0.39
In-ethnicity	1128.25	127.40	1111.33	98.59	1142.36	148.55	-0.80	0.429	0.25
Out-ethnicity	1110.19	137.82	1122.32	137.47	1100.09	140.24	0.52	0.600	-0.16

Note: * *p* < *0.05*

3.1.6.2.4 Supplementary Table 4 Mean accuracies and reaction times in over-writing effect in the congruent condition.

	Whole Sample (n = 44)		Chinese (n = 20)		Germans (n = 24)		*t*	*p*	*d*
	Mean	*SD*	*Mean*	*SD*	*Mean*	*SD*			
Team-based categorization									
Accuracies									
In-ethnicity	83.94	7.86	82.37	8394	85.24	6.76	-1.22	0.231	0.36
Out-ethnicity	80.06	8.30	80.95	9.83	79.32	6.90	0.64	0.525	-0.19
Reaction times									
In-ethnicity	1218.37	101.04	1224.42	110.94	1213.33	94.14	0.36	0.722	-0.11
Out-ethnicity	1268.21	125.48	1198.95	107.60	1325.92	110.56	-3.84***	<0.001	1.16
Ethnicity-based categorization									
Accuracies									
In-team	95.35	5.53	94.66	5.00	95.93	5.98	-0.37	0.713	0.11
Out-team	96.48	5.00	96.52	5.14	96.45	4.99	-0.42	0.676	0.13
Reaction times									

In-team	1030.32	1170.07	1029.04	117.56	1031.39	119.17	-0.07	0.948	0.02
Out-team	1039.79	96.18	1045.65	850.00	1034.90	106.17	0.37	0.717	-0.11

Note: ***p < 0.001

3.1.6.2.5 Supplementary Table 5 Neural correlates of manipulation check (faces > forms across both sessions)

	Cluster size	Hemisphere	MNI-coordinator			t	p
			x	y	z		
Inferior Occipital Gyrus	4932	R	30	-85	-10	17.43	< 0.001
Inferior Occipital Gyrus		L	-27	-85	-4	16.39	< 0.001
Inferior Occipital Gyrus		R	36	-79	-13	16.24	< 0.001
Insula	1867	R	30	23	2	14.26	< 0.001
Inferior Frontal Gyrus		R	45	11	29	12.09	< 0.001
Inferior Frontal Gyrus		R	48	23	29	11.54	< 0.001
Hippocampus	1115	R	24	-34	2	13.1	< 0.001
Hippocampus		L	-24	-31	-1	11.06	< 0.001
Thalamus		R	6	-28	-1	9.72	< 0.001
Precuneus	781	R	9	-70	38	11.56	< 0.001
Precuneus		L	-6	-67	35	10.25	< 0.001
Angular		R	33	-61	44	9.14	< 0.001
Medial Frontal Cortex	482	L	-3	26	44	10.85	< 0.001
Midcingulate Cortex		R	12	26	32	10	< 0.001
Insula	340	L	-33	20	-1	13.74	< 0.001
Medial Frontal Cortex		L	-21	32	-25	9	< 0.001
Midcingulate Cortex	330	R	6	-34	29	12.86	< 0.001
Midcingulate Cortex		L	-6	-22	29	11.47	< 0.001
Midcingulate Cortex		R	6	-1	29	10.64	< 0.001
Middle Frontal Cortex	173	L	-51	20	41	8.26	< 0.001
Middle Frontal Cortex		L	-48	29	41	7.92	< 0.001
Middle Frontal Cortex		L	-36	11	35	6.99	< 0.001
Middle Frontal Cortex	153	L	-42	53	23	7.53	< 0.001
Middle Frontal Cortex		L	-36	47	11	7.15	< 0.001
Middle Frontal Cortex		L	-42	53	14	7.03	< 0.001
Fusiform Gyrus	47	R	30	-4	-34	9.17	< 0.001
Fusiform Gyrus	34	L	-33	-4	-31	8.06	< 0.001
Cerebellum	33	R	18	-37	-43	8.91	< 0.001
Cerebellum	29	L	-18	-37	-43	8.33	< 0.001

Note: significance threshold for whole brain analyses is voxel-wise *p < 0.05 FWE-corrected, k ≥ 10*; L indicates left hemisphere; R indicates right hemisphere.

3.1.6.2.6 Supplementary Table 6 Neural correlates of in-ethnicity versus out-ethnicity faces and its cultural difference.

		Cluster size	Hemisphere	MNI-coordinates			t	p
				x	y	z		
Congruency	*Whole Brain Analyses across All the Participants*							
	None							

	Region of interest Analyses Across all Participants							
	Medial Frontal Gyrus	111	R	18	-1	53	4.15	0.039
	Chinese > Germans							
	Whole Brain Analyses							
	Middle Occipital Gyrus	22	L	-9	-100	11	6.68	< 0.001
	Region of Interest Analyses							
	Medial Frontal Gyrus	137	R	3	35	-16	4.34	0.025
	Germans > Chinese							
	Whole Brain Analyses							
	Middle Occipital Gyrus	102	R	12	-94	8	7.47	< 0.001
	Region of Interest Analyses							
	None							
	Whole Brain Analyses/ Region of Interest Analyses across All Participants							
	None							
	Chinese > Germans							
	Whole brain analyses							
Incongruency > Congruency	Middle Occipital Gyrus	66	R	12	-97	14	6.96	0.001
	Region of Interest Analyses							
	None							
	Germans > Chinese							
	Whole Brain Analyses							
	Middle Occipital Gyrus	100	L	-12	-100	14	7.87	< 0.001
	Region of Interest Analyses							
	None							

Note: significance threshold for whole brain analyses is voxel-wise *p < 0.05 FWE-corrected, k ≥ 10*; and for the region of interest analyses is voxel-wise *p < 0.05 small volume correction, k ≥ 10*; L indicates left hemisphere, R indicates right hemisphere.

3.1.6.2.7 Supplementary Table 7 Neural correlates of in-team versus out-team faces and its cultural difference.

		Cluster size	Hemisphere	MNI-coordinates			t	p
				x	y	z		
	Whole Brain Analyses Across all Participants							
	None							
	Region of Interest Analyses across All Participants							
Congruency	Medial Frontal Gyrus	330	L	-15	47	20	4.20	0.031
	Chinese > German/ German > Chinese							
	Whole Brain Analyses/ Region of Interest Analyses							
	None							
Incongruency	*Whole Brain Analyses/ Region of Interest Analyses across All Participants*							

> Congruency	None
	Chinese > German/ German > Chinese
	Whole Brain Analyses/ Region of Interest Analyses
	None

Note: significance threshold for whole brain analyses is voxel-*wise p < 0.05 FWE-corrected, k ≥ 10*; and for the region of interest analyses is voxel-wise *p < 0.05 small volume correction, k ≥ 10*; L indicates left hemisphere, R indicates right hemisphere.

3.1.6.2.8 Supplementary Table 8 Neural correlates of in-ethnicity versus in-team faces.

	Cluster size	Hemisphere	MNI-coordinates			t	p
			x	y	z		
Whole Brain Analyses							
Superior Temporal Gyrus	5367	R	51	-31	20	11.36	< 0.001
Superior Parietal Lobe		R	21	-43	65	10.53	< 0.001
Middle Temporal Gyrus		R	54	-64	23	10.47	< 0.001
Middle Temporal Gyrus	3082	L	-51	-64	23	12.1	< 0.001
Middle Temporal Gyrus		L	-63	-7	-7	12.01	< 0.001
Superior Temporal Gyrus		L	-39	-19	17	11.28	< 0.001
Superior Frontal Gyrus	663	L	-12	38	50	8.43	< 0.001
Superior Frontal Gyrus		L	-24	23	44	8.36	< 0.001
Superior Frontal Gyrus		L	-12	62	20	7.71	< 0.001
Cerebellum	101	R	21	-88	-34	8.23	< 0.001
Superior Occipital Lobe	54	L	-3	-88	26	6.27	0.004
Superior Occipital Lobe		R	6	-76	26	5.80	0.014
Inferior Frontal Gyrus	21	L	-45	32	-10	6.27	0.004
Superior Occipital Lobe	17	R	15	-88	29	6.38	0.003
Superior Frontal Gyrus	14	R	9	59	26	5.88	0.011
Region of Interest Analyses							
Amygdala	30	L	-27	-4	-25	3.23	0.020
Amygdala	41	R	21	-7	-22	4.77	< 0.001

Note: significance threshold for whole brain analyses is voxel-wise *p < 0.05 FWE-corrected, k ≥ 10*; and for the region of interest analyses is voxel-wise *p < 0.05 small volume correction, k ≥10*; L indicates left hemisphere, R indicates right hemisphere.

3.1.6.2.9 Supplementary Table 9 Neural correlates of in-team versus in-ethnicity faces.

	Cluster size	Hemisphere	MNI-coordinates			t	p
			x	y	z		
Whole Brain Analyses							
Middle Frontal Gyrus	324	R	48	38	32	7.82	< 0.001
Middle Frontal Gyrus		R	51	32	38	7.49	< 0.001
Middle Frontal Gyrus		R	39	17	62	7.00	< 0.001
Superior Parietal Lobe	278	R	33	-58	50	8.44	< 0.001
Insula	198	R	33	23	-1	10.37	< 0.001

Inferior Frontal Lobe		R	21	35	-7	6.88	0.001
Cerebellum	174	L	-33	-70	-43	9.18	< 0.001
Cerebellum		L	-27	-64	-28	5.99	0.008
Cerebellum		L	-36	-67	-31	5.95	0.009
Cerebellum	156	L	-9	-79	-25	8.69	< 0.001
Cerebellum		R	6	-76	-28	6:19	0.005
Medial Frontal Gyrus	103	R	3	29	41	7.17	< 0.001
Medial Frontal Gyrus		R	9	29	35	7.11	< 0.001
Medial Frontal Gyrus		L	-9	29	38	5.78	0.015
Insula	88	L	-30	20	-1	9.13	< 0.001
Middle Occipital Gyrus	14	R	33	-82	5	6.49	0.002
Cerebellum	13	R	0	-58	-28	5.96	0.009
Region of Interest Analyses							
Fusiform Gyrus	206	R	39	-49	-16	4.62	0.005
Fusiform Gyrus	121	L	-36	-55	-13	4.89	0.002
Medial Frontal Gyrus	155	R	3	29	41	5.89	< 0.001
Medial Frontal Gyrus	114	L	-3	29	41	7.17	< 0.001

Note: significance threshold for whole brain analyses is voxel-wise *p < 0.05 FWE-corrected, k ≥ 10*; and for the region of interest analyses is voxel-wise *p < 0.05 small volume correction, k ≥ 10*; L indicates left hemisphere, R indicates right hemisphere.

3.1.6.2.10 Supplementary Table 10 Neural correlates of out-ethnicity versus out-team faces.

	Cluster size	Hemisphere	MNI-coordinates			t	p
			x	y	z		
Middle Temporal Gyrus	2403	L	-51	-16	-25	11.51	< 0.001
Middle Temporal Gyrus		L	-57	-25	-7	10.92	< 0.001
Middle Temporal Gyrus		L	-60	-16	-7	10.7	< 0.001
Middle Temporal Gyrus	2010	R	60	-10	-22	10.04	< 0.001
Middle Temporal Gyrus		R	51	11	-31	9.9	< 0.001
Middle Temporal Gyrus		R	60	-61	32	8.52	< 0.001
Medial Frontal Gyrus	1536	R	0	41	-19	9.62	< 0.001
Medial Frontal Gyrus		L	-3	20	-22	9.14	< 0.001
Medial Frontal Gyrus		L	-6	32	-19	8.84	< 0.001
Superior Parietal Lobe	485	R	6	-31	62	7.16	< 0.001
Superior Parietal Lobe		R	18	-40	74	7.1	< 0.001
Superior Parietal Lobe		R	24	-28	74	7.08	< 0.001
Cerebellum	43	R	27	-85	-34	6.82	0.001
Middle Cingulate Cortex	17	R	0	-49	35	5.76	0.014

Note: significance threshold for whole brain analyses is voxel-wise *p < 0.05 FWE-corrected, k ≥ 10*; L indicates left hemisphere, R indicates right hemisphere.

3.1.6.2.11 Supplementary Table 11 Neural correlates of out-team versus out-ethnicity faces.

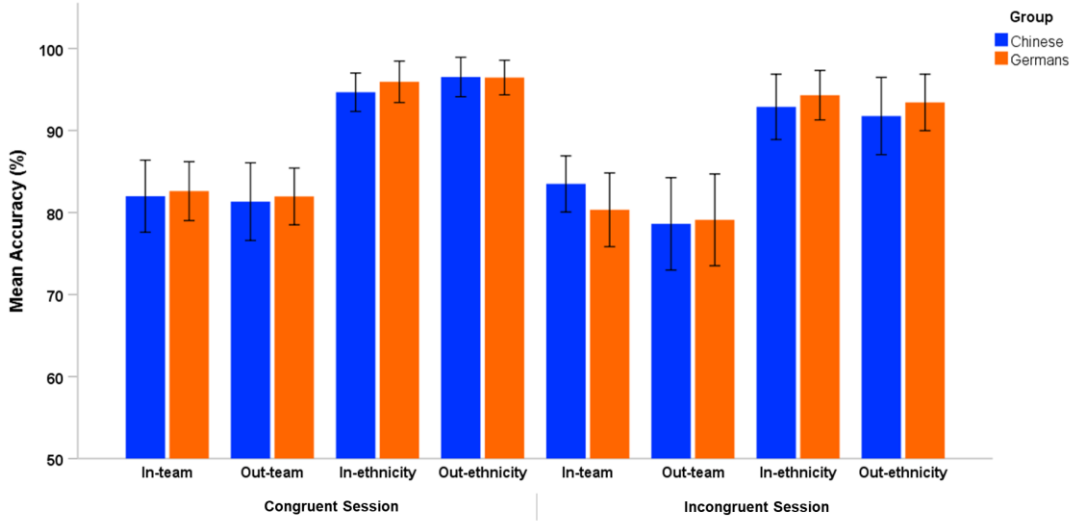
	Cluster size	Hemisphere	MNI-coordinates			t	p
			x	y	z		
Superior Parietal Lobe	625	R	33	-58	56	8.98	< 0.001
Superior Occipital Gyrus		R	24	-64	44	8.65	< 0.001
Middle Occipital Gyrus		R	30	-67	32	8.51	< 0.001

Inferior Frontal Gyrus	388	R	42	8	29	8.20	< 0.001
Middle Frontal Gyrus		R	48	35	32	7.40	< 0.001
Middle Frontal Gyrus		R	54	29	35	7.37	< 0.001
Superior Frontal Gyrus	255	R	3	23	50	8.61	< 0.001
Middle Cingulate Cortex		R	12	26	35	7.82	< 0.001
Insula	220	R	33	26	2	12.48	< 0.001
Cerebellum	219	L	-9	-76	-25	8.55	< 0.001
Cerebellum		R	9	-73	-25	6.30	0.003
Cerebellum		R	0	-61	-31	6.21	0.004
Middle Occipital Gyrus	155	L	-21	-64	32	7.06	< 0.001
Superior Occipital Gyrus		L	-12	-67	32	6.61	0.001
Cerebellum	136	L	-30	-70	-46	8.00	< 0.001
Cerebellum		L	-30	-64	-31	6.36	0.003
Insula	133	L	-30	23	-1	10.73	< 0.001
Hippocampus	131	R	9	-22	-10	8.31	< 0.001
Middle Frontal Gyrus	105	L	-42	2	35	7.95	< 0.001
Inferior Frontal Gyrus		L	-30	2	29	6.25	0.004
Thalamus	69	R	18	-1	20	6.38	0.002
Thalamus		R	6	-10	5	6.20	0.004
Thalamus		R	15	-7	14	5.84	0.011
Middle Frontal Gyrus	66	R	33	5	50	7.38	< 0.001
Inferior Temporal Gyrus	43	R	45	-70	-10	6.09	0.006
Inferior Temporal Gyrus		R	48	-58	-13	5.91	0.009
Inferior Parietal Gyrus	36	L	-36	-49	44	6.34	0.003
Middle Occipital Gyrus	29	L	-27	-88	8	6.25	0.003
Insula	12	L	-21	2	20	5.81	0.012

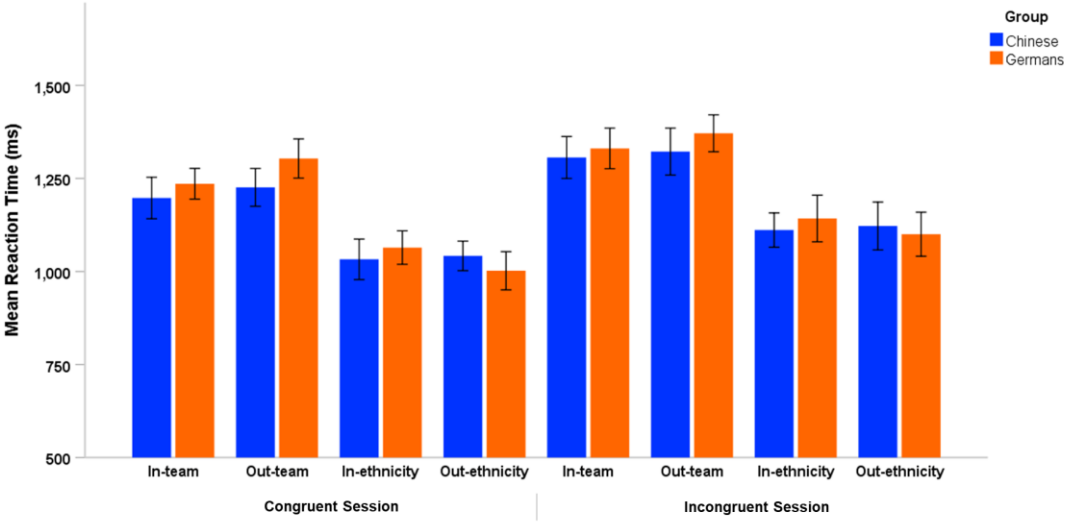
Note: significance threshold for whole brain analyses is voxel-wise $p < 0.05$ *FWE-corrected,* $k \geq 10$; L indicates left hemisphere, R indicates right hemisphere.

3.1.6.3 Supplementary figures

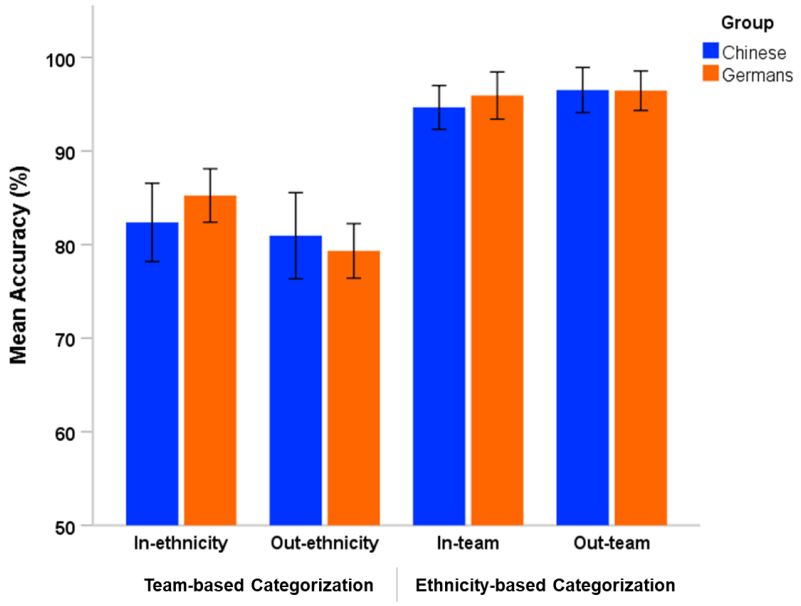
3.1.6.3.1 Supplementary Figure 1. Mean accuracy (%) in the social categorization task.



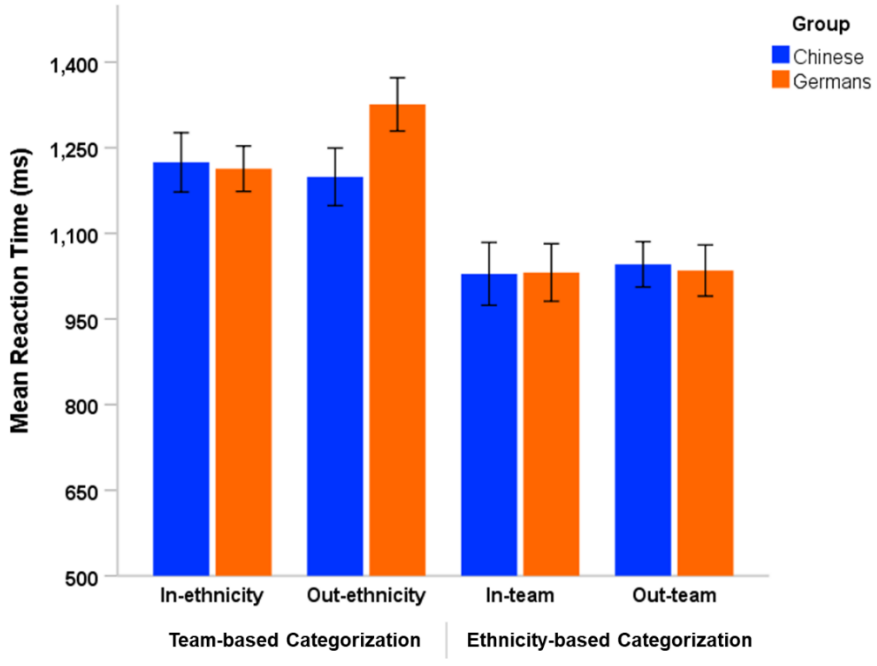
3.1.6.3.2 Supplementary Figure 2. Mean reaction times (ms) in the social categorization task.



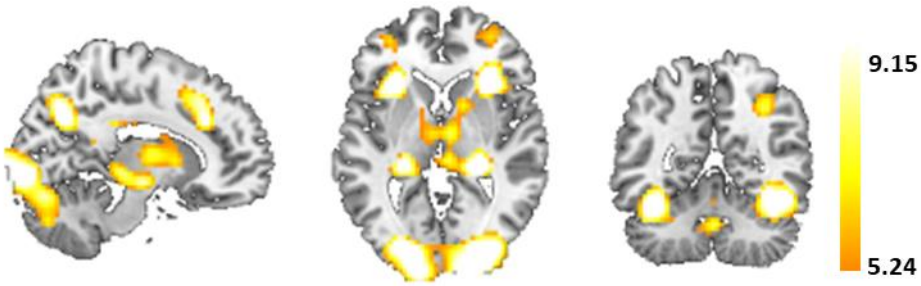
3.1.6.3.3 Supplementary Figure 3. Over-writing effect on accuracy.



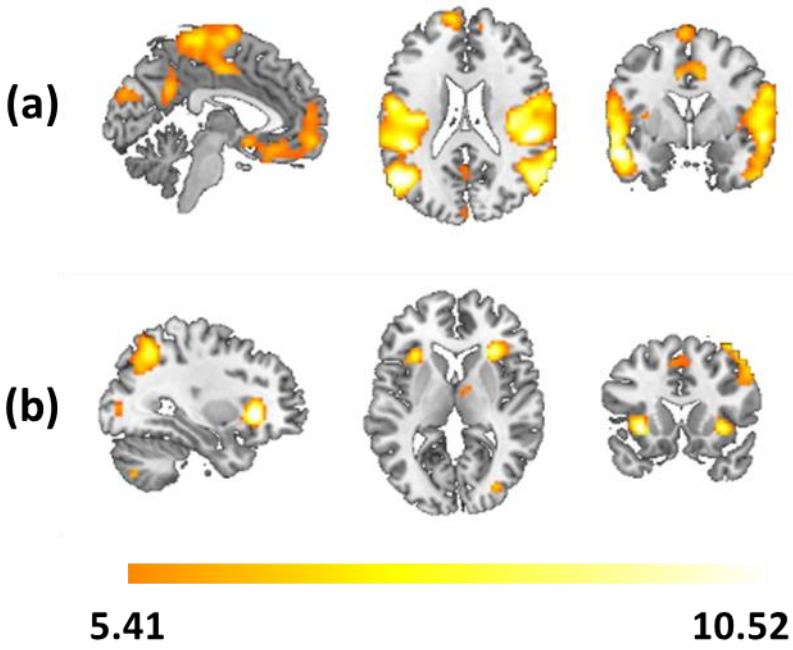
3.1.6.3.4 Supplementary Figure 4. Over-writing effect on reaction times.



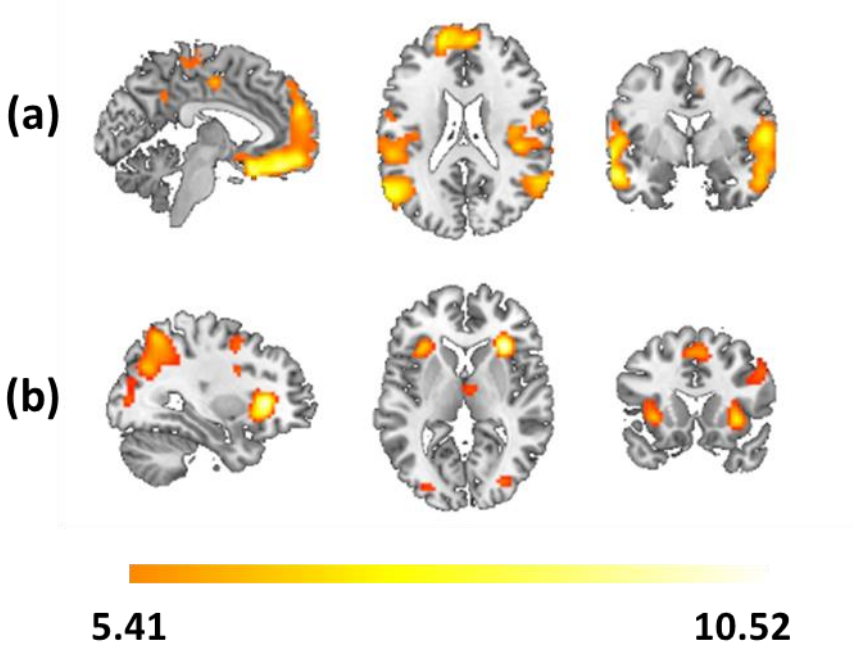
3.1.6.3.5 Supplementary Figure 5. Neural correlates of manipulation check (faces > forms). Note: threshold for displaying is voxel-wise *p < 0.05 FWE-corrected, k ≥ 10*.



3.1.6.3.6 Supplementary Figure 6. Neural correlates of in-ethnicity > in-team (a) and in-team > in-ethnicity (b). Note: threshold for displaying is voxel-wise *p < 0.05 FWE-corrected, k ≥ 10*.



3.1.6.3.7 Supplementary Figure 7. Neural correlates of out-ethnicity > out-team (a) and out-team > out-ethnicity (b). Note: threshold for displaying is voxel-wise $p < 0.05$ *FWE-corrected,* $k \geq 10$.



4 GENERAL DISCUSSION

The past decades have witnessed a huge expansion of studies on social cognition with neuroscience approaches. Although some studies initiated understanding the social cognition by conceiving its structure, there are still several open questions. The present dissertation aimed at advancing the knowledge on social cognition from the perspective of what influences social cognition. Accordingly, the possible impact factors of social cognition have been grouped into two main domains according to the inter-individual variabilities in present dissertation. One is from the microscopic level of the individual, discussing how pathological risk factors affect social cognition in the healthy population who are from the same ethnicity; the other one is from the macroscopic level of the group, by comparing the responses to social cognition between people from distinct cultural backgrounds. Based on such perspectives, study one focused on the individual level by exploring whether and how schizotypy and schizophrenia risk allele (*ZNF804A rs1344706*) influence the neural basis of social cognition in healthy participants with a fine-designed paradigm including aToM, emotion recognition, neutral face processing, and a non-social control condition. Study two was conducted to assist in understanding the social cognition from the group level. According to the assumption that the differences in higher-order social processes between cultures might be caused by the differentiation of basic social processes, cultural differences in intracultural advantage during basic social categorization were investigated by applying a social categorization fMRI-task with facial stimuli from Asians and Caucasians to two groups of participants who are typically from individualistic (German) and collectivistic (Chinese) background.

4.1 Summary of study results

4.1.1 Understanding social cognition from the individual perspective

Study one conducted a social-cognitive task to investigate the associations of neural correlates of social cognition with schizophrenia risk factors. The findings from study one add evidence to the microscopic perspective that personality traits and genetic

variants influence neural correlates of social cognition, suggesting aberrant pSTS functioning during social-cognitive processing an interesting endophenotype for schizophrenia.

First, results of study one replicated previous findings (Mier et al., 2017; Mier, Lis, et al., 2010) demonstrating enhanced activation in pSTS and BA 44 with increasing social-cognitive demands across participants (from neutral faces processing over emotion recognition to aToM), highlighting the functioning of pSTS and BA 44 in higher-order social cognition, such as aToM. Such findings further underlined the importance of pSTS in inferring others' mind and intentions (Gallagher & Frith, 2003).

The results further showed the neural correlates of social cognition varying with the schizotypy (Abu-Akel et al., 2017; Y. Wang et al., 2015) and differentiating between schizophrenia risk-allele carriers and non-risk-allele carriers (Esslinger et al., 2009; H. Walter et al., 2011) in the general population. Interestingly, the associations of enhanced pSTS activation with schizophrenia risk allele and schizotypy were found only when processing neutral (non-intentional) faces, illustrating people with increasing proneness to schizophrenia demonstrating a tendency to wrongly perceiving emotions and intentions from non-emotional/non-intentional stimuli. It further suggests the aberrant pSTS functioning for neutral social stimuli probably presenting the endophenotype for hyper-mentalizing (Abu-Akel et al., 2017; Ciaramidaro et al., 2014; H. Walter et al., 2011). Moreover, such finding also adds evidence to previous conclusions that impairments in higher-order social cognition may be caused by the aberrant or impaired basic social-cognitive processes (Mier et al., 2017; Mier, Sauer, et al., 2010).

In terms of which specific facet of schizotypy is associated with the pSTS dysfunction for neutral stimuli, the results pointed out individuals with higher self-reported scores on disorganization and positive symptoms (this association was marginally significant) presenting greater activation in pSTS in response to neutral stimuli. In addition, the connectivity results also showed a positive correlation between disorganization symptoms and pSTS inter-hemisphere connectivity for processing neutral versus non-social stimuli. Positive symptoms refer to symptoms which are in excess or added to normal mental functioning, such as delusions and hallucinations (Abu-Akel et al.,

2017). Increased positive symptoms might lead to an impairment in perceiving neutral stimuli in a correct fashion, resulting in false inputs during early stages of social perception (Kapur, 2003; Kapur et al., 2005). Disorganization symptoms are linked to obvious impairments in cognitive abilities (Uhlhaas et al., 2006). The increased self-reported disorganization and positive symptom scores may illustrate less ability to exert a cognitive influence on false perceptions of social stimuli probably caused by increased positive symptoms (Phillips & Silverstein, 2003).

Taken together, these results may suggest that hyper-mentalizing in response to neutral stimuli might be a consequence of erroneous perception and cognitive deficits (Mier & Kirsch, 2015). Importantly, our findings also demonstrated neural responses to social cognition varied with schizophrenia risk factors in healthy participants, supporting the microscopic perspective on the individual to deepen the knowledge of the neural correlates of social cognition and their role in schizophrenia.

4.1.2 Understanding social cognition from the group perspective

Study two used the cultural neuroscience approach aimed at investigating cultural differences in in-ethnicity and in-team bias, and to explore how in-ethnicity bias can be reduced by the novel in-team bias. Results highlighted the importance of the MFC in social categorization and showed cultural differences in the neural responses during ethnicity-based categorization, but no neural difference was found during team-based categorization between cultures. In addition, the results suggest that the in-ethnicity bias is not easily over-written by the in-team bias across cultures.

Behaviorally, intracultural advantage/other-ethnicity categorization advantage during ethnicity-based face categorization was found only in the German group. However, inconsistent with the hypotheses, results did not show a comparable behavioral pattern in the Chinese group. It might be attributed to the recruitment of the Chinese participants who are studying or living in Germany while the experiments implemented. Since the exposure to the opposite culture and intercultural communication may influence the facial perception of people who are from the opposite culture (Derntl, Habel, et al., 2009; Derntl et al., 2012), it might reduce the extent of salience of perceiving faces from the opposite culture, which eventually results in the fact that the

intracultural advantage in ethnicity-based categorization was not observed in the Chinese group.

However, increased dorsal MFC activation was found in response to in- versus out-ethnicity categorization across groups. As the dorsal part of the MFC is associated with self-identity processes (D'Argembeau et al., 2007; Jenkins & Mitchell, 2011), increased dorsal MFC activation might be interpreted as the neural basis of the intracultural advantage in both groups. Interestingly, the results also revealed higher ventral MFC activation for in- versus out-ethnicity categorization in the Chinese group than the German group. Since the ventral part of MFC is linked to represent the preference of stimuli in an unconscious or automatic fashion (Levy et al., 2011), this result may illustrate higher neural preference of in-ethnicity faces during ethnicity-based categorization in the Chinese group than the German group.

In terms of team-based categorization, the in-team bias was observed only in the German group, but not in the Chinese group on the behavioral level. Such findings may add evidence to the idea that people from the collectivistic background present difficulties to develop team memberships without pre-existing personal ties and contact to the potential members (Brewer & Yuki, 2007). However, the neural results presented increased activation in the dorsal MFC for in-team relative to out-team categorization, suggesting an in-team bias across both cultural groups on the neural level. Since significant neural differences between groups were not found while contrasted in-team to out-team categorization, it may suggest dorsal MFC probably being a common neural code for processing in-team members across cultural groups.

In addition, study two also contributed to revealing the differences between the team- and ethnicity-based categorization. Behaviorally, the RTs in team-based categorization were longer than the RTs in ethnicity-based categorization. On the neural level, results demonstrated increased activation in the default mode network and amygdala for ethnicity- versus team-based categorization across both cultural groups, whereas elected activation in the MFC and FFG for the team- versus ethnicity-based categorization. Taken together, such findings support the assumption that ethnicity-based and team-based categorization may present different dimensions of social

categorization (such as perceptual- and knowledge-based categorization), leading to ultimately distinct neural paths (Mattan et al., 2018).

Taken together, the results of study two underlined the importance of MFC activity during social categorization across cultural groups, suggesting a common neural code for social categorization across cultures. In terms of the basic and perceptual-based social categorization (ethnicity-based categorization), both groups showed in-ethnicity bias on the neural level, but the Chinese group showed higher MFC activation for categorizing in-ethnicity versus out-ethnicity faces in comparison to the German group. These results suggest higher in-ethnicity favoritism and deeper processing of in-ethnicity members in the Chinese group (although it was not observed on the behavioral level). With respect to the complicated and knowledge-based social categorization (team-based categorization), increased MFC activation was observed in both groups for categorizing in-team versus out-team members, but no group difference was found in the neural responses during team-based categorization, while in-team bias was demonstrated in the German group but not in the Chinese group on the behavioral level. Such findings might indicate culture exerts influence more on the basic and perceptual-based social categorization on the neural level, but not on the complicated and knowledge-based social categorization. In short, the findings from study two revealed the differences in neural responses during in-ethnicity facial processing, which support the macroscopic perspective that culture might influence the neural correlates of social cognition.

4.2 A new framework for understanding the neural correlates of social cognition

As mentioned above, social cognition has been defined as a series of mental operations underlying social interactions (Brothers, 1996; Happé et al., 2017). A complex social-cognitive process is usually established on the interactions of several simple and basic social-cognitive processes. And these cognitive subprocesses are specific for processing particular social information/cues (Brothers, 1996). Based on this assumption, social cognition can be roughly divided into three different domains (see Figure 2): Lower-order social cognition, higher-order social cognition, and social performances/outputs. The lower-order/basic processes of social cognition are linked to the perception of social cues and primary embodied cues, such as categorization of

self and others, which is associated with STS (Allison, Puce, & McCarthy, 2000) and brain regions of the salience network including amygdala, insula, and striatum (Rilling et al., 2008). The higher-order/advanced processes of social cognition are undertaken to understand or deepen processing those social cues which are encoded in the basic social-cognitive processes phase, such as empathy, mentalizing, and self-reference processing. And those processes of social cognition at this level are linked to the brain regions of the mentalizing network (e.g. MFC and MNS, (Frith & Frith, 2006; Rizzolatti & Craighero, 2004).), the cognitive-control network (e.g. temporal sulcus and MFC (Cole & Schneider, 2007)), and the self-network (e.g. medial prefrontal regions (Meer et al., 2010)). By relying on the integration of the information from these distinct levels of processes, a complex social output/performance, i.e. a social behavior, is formed which can be seen in daily social life. When an impaired social output/response happens, the causes might be traced back to deficits in the underlying social-cognitive processes (Mier et al., 2017; Mier, Sauer, et al., 2010).

The present section attempts to propose a view to advance the understanding of neural correlates of social cognition from the perspective on what influences social cognition with taken the microscopic and the macroscopic view into account.

In terms of the microscopic domain, personality, pathological traits and genetic variants could be considered as powerful impact factors related to neural correlates of social cognition. Such indicators directly or indirectly link to developing an individual system of social attentions (Bartz, Zaki, Bolger, & Ochsner, 2011; Shamay-Tsoory & Abu-Akel, 2016), affecting how a person perceives and encodes social cues in a more automatic and unconscious fashion. It might be assumed that these indicators from the microscopic domain are more linked to the sensory inputs and information encoding, which is related to the basic social-cognitive processes. Genes and neurotransmitters represent neurobiological individual factors influencing the neural patterns of social cognition. For example, oxytocin, a peptide hormone and neuropeptide, can decrease amygdala activation and reduce coupling of the amygdala to brainstem regions for automatic fear perception (Kirsch et al., 2005; Petrovic, Kalisch, Singer, & Dolan, 2008). And the results of study one in the present dissertation also support this idea. Differences in STS activation for neural facial processing between carriers and non-

carriers of schizophrenia genotype indicate that the individual pathological traits may influence the neural correlates of social perception.

With respect to the macroscopic domain, culture and environment are the most obvious factors related to the neural correlates of social cognition. They play a vital role in influencing a person's value and the manner to understand and to interpret social cues. This might illustrate a closer connection of the factors of the group level with higher-order processes of social cognition, although study two was conducted to focus on the basic process of social cognition and revealed a cultural influence on the neural correlates of in-ethnicity categorization. In line with the idea that group influences on social cognition prominently affect higher-order processes of social cognition, a study of Zhu and colleagues reported activation in the "self-network" to represent the self and their mother in a group of Chinese participants, but the same activation pattern was found only for self-processing in Westerners (Zhu et al., 2007). They conclude that culture modulates the neural representatives of self-references which is a higher-order process of social cognition associated with thinking style (Zhu et al., 2007). Findings of de Greck and colleagues also add support to this idea (de Greck et al., 2012). They applied an empathy task to Chinese and Germans and found the German group showed increased activation in the regions of the MNS for empathizing with angry facial expression of people from their own ethnicity, whereas the Chinese group showed enhanced activation in the brain regions related to the control network while empathizing with their own-ethnicity angry faces. They interpreted such neural differences according to the distinct social rules between cultures that people from the collectivism shed more light on the harmony during social interaction than people from the individualism (Markus & Kitayama, 1991) resulting in a suppression of anger to maintain harmony in the Chinses group. Notably, the different neural basis of empathizing with anger might also related to the differences in the way of automatic facial processing between cultures. This might indicate that the indicators of neither the microscopic nor the macroscopic perspective affect social cognition independently, but interplay with each other to exert joint influences on social outputs/performances (Grabe et al., 2012).

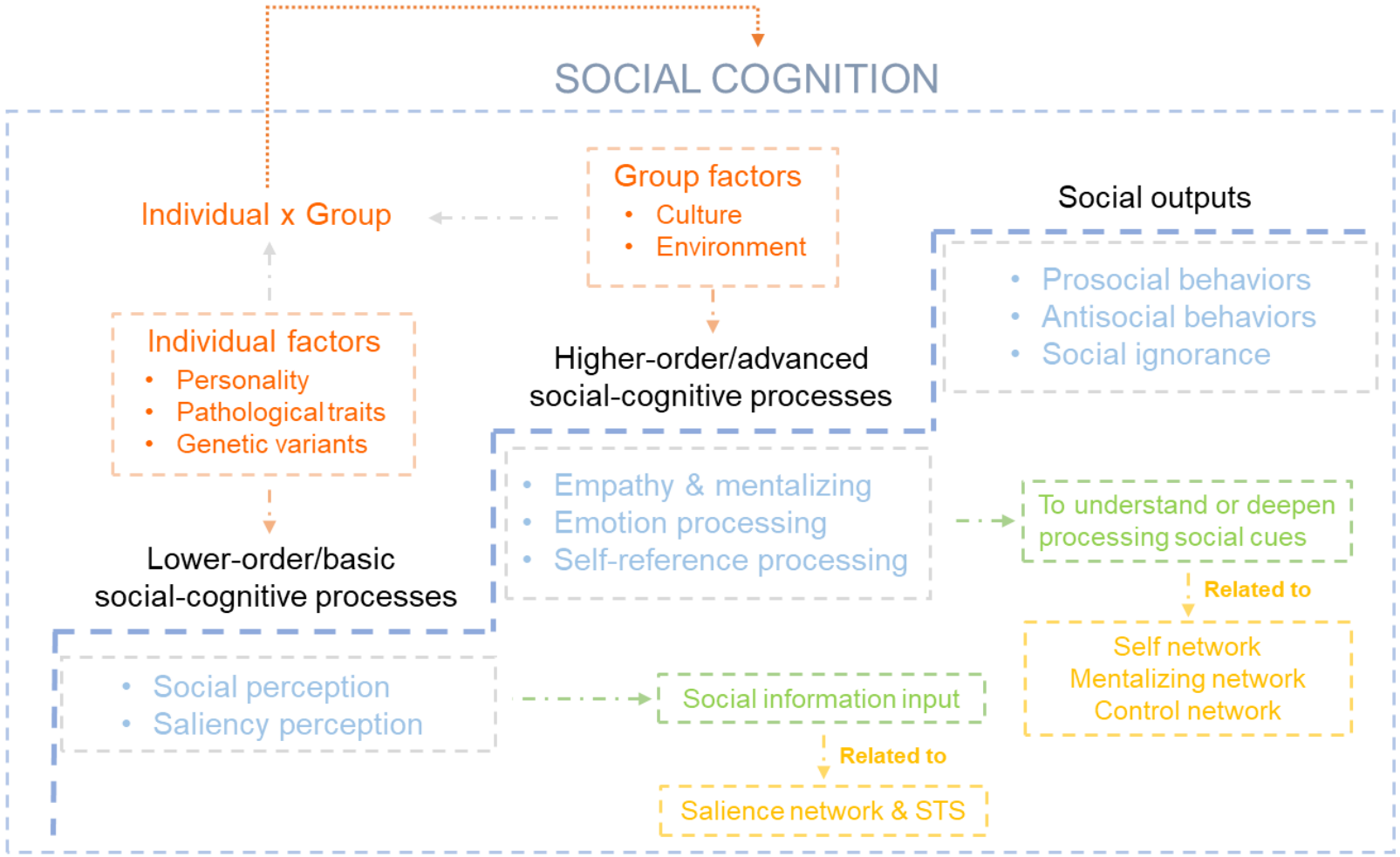


Figure 2. A framework to understand the neural correlates of social cognition. The sub-categorizations of social cognition are written in black; their related processes of social cognition in blue; their functioning in green; their related brain network in yellow; and their impact factors in orange. Note: STS indicates superior temporal sulcus.

Thus, both the microscopic, as well as the macroscopic perspective should be taken into account when aiming at understanding social cognition. However, modeling the interaction between the individual and the group factors is challenged by the wide range of the impact factors of social cognition which must be investigated. Existing pieces of literature initiated to explore such interaction effects on social cognition by mostly focusing on the gene x life experience interaction. For example, a study of Beaver and colleagues found the 10R allele of the dopamine transporter (DAT1) gene interacts with high-risk environment jointly working on the formation of peer affiliation (Beaver, Wright, & DeLisi, 2008). The G-allele carriers of oxytocin rs53576 polymorphism was shown to interact with high social stress, which may increase the level of antisocial behaviors (Smearman, Winiarski, Brennan, Najman, & Johnson, 2015). With this regard, the in-ethnicity bias might also be interpreted as a consequence of the interactions between gene and environment. An association between in-ethnicity bias and oxytocin has been well-documented (De Dreu, Greer, Van Kleef, Shalvi, & Handgraaf, 2011),and the environmental factors, such as exposure to the other culture or integration to other cultures, might alter a person's in-ethnicity bias, or even lead to the development of an other-ethnicity bias (Derntl, Habel, et al., 2009). However, the extent of integration to one culture is assumed to be associated with the openness of the host culture. That is, in-ethnicity bias could be affected by the individual oxytocin level, which might be modulated by the interaction of individual openness to the host culture with the cultural openness to the individual, representing a highly complex interaction between genetic variants, personality traits, and cultural traits.

Taken together, in line with the idea of Brother (Brothers, 1996), I conclude that social cognition consists of a series of social processes with different extent of complexity. On the basis of the inter-individual variabilities, I proposed a framework to advance the understanding on the neural correlates of social cognition by grouping its impact factors into two domains: microscopic perspective on the individual and macroscopic perspectives on the group. Although indicators of the microscopic and the macroscopic level might shed light on different domains of social processes, they interplay with each other to influence the social performances, or even a basic social process.

4.3 Limitations and future studies

Although the present dissertation advances the knowledge of neural correlates of social cognition with a new frame including a so-called microscopic and a so-called macroscopic level, some continuous efforts are still needed.

In terms of the microscopic domain, study one was set up to investigate the neural differences in social cognition among individuals with the idea of testing the differences in pathological personality traits and pathological risk genes in the general population. As mentioned, only one risk SNP of schizophrenia was tested in the present dissertation, future studies could explore the load of risk SNPs to reveal biological subcategories of schizophrenia (Ehrenreich et al., 2018). Further, the social cognition task applied in the present dissertation only contains parts of social processes (Mier et al., 2017; Mier, Lis, et al., 2010), the other types of complex social cognition should also be taken into consideration, such as empathy and emotion regulation (Green et al., 2015). In addition, there is a wide range of individual personality traits, from the typical BIG FIVE (Digman, 1990) to pathological traits, whereas the present dissertation only investigated the association of neural correlates of social cognition with schizotypy, one of the pathological traits. Future studies could take other domains of personality traits into account, such as big five or autistic traits, to advance the knowledge of neural correlates of social cognition from the microscopic perspective.

With respect to the macroscopic domain, study two was conducted to explore the differences in neural correlates of basic social processes between ethnicities, more research is needed to explore the cultural differences in higher-order social processes during social interaction, especially during those social interactions with pronounced different cultural meanings, such as feeling of embarrassment (Singelis & Sharkey, 1995; Wan, 2013). Besides, study two did not picture significant linear changes of the neural responses to categorizing other- and own-ethnicity faces with an accelerated duration of exposure to the German culture in the Chinese sample. Future studies could think of recruiting two groups of participants who are from the same ethnicity, but one exposes to the opposite culture while the experiment implements. With this design, researchers cannot only draw conclusions how neural representations of social processes change with the duration of exposure to the opposite culture in the exposure

group (like study two) but also test the exposure effect on the neural responses to social processes by directly comparing the data from the two groups. Furthermore, certain studies have assumed that the extent of integrating into the host culture (so-called acculturation), rather than simply being exposed to it, might exert greater influence in altering individuals' core cultural values and changing the behavioral and neural responses to people who are from the host culture during social interaction (Berry, 2007). Thus, future studies could gain more efforts first on developing measurements assessing the extent of individuals' cultural integration to the host culture, then on detecting the acculturation effect on the social cognition while people interact with others of the host culture.

In addition, both studies to explore what influences the neural correlates of social cognition used a cross-sectional approach. Associations of neural responses during social cognition with schizotypy were found in study one, but it is impossible to know whether schizotypy causes the aberrations in pSTS during processing of neural facial expressions or the other way around. Thus, future investigations are needed to causally investigate the associations between schizotypy and neural correlates of social cognition with longitudinal studies.

4.4 Implications for psychotherapeutic Interventions

Since a comprehensive model for psychopathology yield to the integration of many distinct domains comprising genetics, neurobiology, cognitive mechanisms, and sociocultural frameworks (Choudhury & Kirmayer, 2009), the perspectives of understanding social cognition in the present dissertation can also be applied to advance the theories of psychopathology and develop effective and efficient strategies to cope and heal mental disorders. For instance, study one in the present dissertation revealed the right pSTS might represent an endophenotype during social cognition in schizophrenia within a German sample. This finding may contribute to developing neurofeedback therapies targeting at manipulating right pSTS activation during social cognition to avoid developing a negative bias and a negative attribution style, and possibly schizophrenia in Caucasians. However, for advocating such promising neurotherapy in a more generalized fashion, the right pSTS dysfunction during social cognition first has to be replicated in another-ethnicity sample. If it cannot be replicated

with other-ethnicity samples, it is inevitable to develop more cultural-specific psychotherapeutic trainings to prevent people from psychosis or heal people with psychosis. In short, the perspective proposed in the present dissertation might be a promising fashion to address the huge challenge for diagnosis of mental disorders, theories of psychopathology, as well as effective intervention strategies to mental health due to the differences in mental health across distinct nations, ethnicities and cultures (Choudhury & Kirmayer, 2009).

5 SUMMARY

Social cognition, as of the fundament of social interaction, is central to our daily social life. Although the past two decades have witnessed a huge increase in academic interest in social cognition, knowledge of the neural correlates of social cognition is still limited. With a growing number of studies investigating social cognition with a neuroscientific approach, a well-framed structure based on systematic perspectives to understand social cognition is urgently needed. The present dissertation attempted to investigate social cognition from two domains based on the idea what influences social cognition, the so-called microscopic perspective on the individual and the macroscopic perspective on the culture.

From the microscopic perspective, the effects of schizophrenia risk factors (including schizotypy and *rs1344706 SNP*) on neural correlates of social cognition were investigated in a healthy German sample. The results show associations between schizotypy, as well as the risk allele of the *rs1344706* SNP and pSTS activation in response to neutral facial stimuli, suggesting right pSTS dysfunction in response to neural social stimuli might present an endophenotype for schizophrenia. Furthermore, these findings give evidence on the microscopic perspective proposed above that neural correlates of social cognition can be influenced by risk factors for mental illnesses in healthy participants.

Regarding the macroscopic perspective, the cultural effects on neural responses to different facets of social categorization were investigated with participants from different ethnicities. During the ethnicity-based categorization, the Chinese group showed higher ventral MFC activation for categorizing in-ethnicity versus out-ethnicity faces than the German group, even in-ethnicity bias was not observed in the Chinese group on the behavioral level. Since ventral MFC is well-documented to be associated with representing the preference of stimuli even in an unconscious or automatic fashion, the increased ventral MFC activation in the Chinese group may indicate that they present higher in-ethnicity preference than the German group. Further, increased dorsal MFC activation in response to in-team versus out-team faces was found in both ethnic groups during team-based categorization, inferring that the dorsal MFC might be a generalized neural code for encoding in-team members across ethnicities. In

addition, by comparing the contrasts of in-team versus in-ethnicity and out-team versus out-ethnicity, the results suggest that ethnicity-based and team-based categorization probably presenting different dimensions of social categorization (such as perceptual- and knowledge-based categorization).

To summarize, the present dissertation aimed to advance the understanding of social cognition from microscopic and macroscopic perspectives. Such an approach might transfer to the clinical and psychotherapeutic field for developing more generalized interventions and treatments across ethnicities to prevent people from mental disorders or to optimize interventions for people with mental illnesses.

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7 PUBLICATIONS

Yan, Z., Schmidt, S. N.L., Frank, J., Witt, S. H., Hass, J., Kirsch, P. & Mier, D. (submitted). Hyperfunctioning of right posterior superior temporal sulcus in response to neutral facial expressions presents an endophenotype of schizophrenia.

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8 CURRICULUM VITAE

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