Investigating Social Cognition: Lessons from the Perception of Dynamic Nonverbal Cues in Cross-Cultural Psychology and High-Functioning Autism

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List of Abbreviations

Brain Regions:

dlPFC	Dorsolateral prefrontal cortex
dmPFC	Dorsomedial prefrontal cortex
FG	Fusiform gyrus
IFG	Inferior frontal gyrus
PCC	Posterior cingulate cortex
STS	Superior temporal sulcus
vmPFC	Ventromedial prefrontal cortex

Other:

3D	Three-dimensional
ANOVA	Analysis of variance
BOLD	Blood-oxygen level dependent
EMG	Electromyography
EPN	Emotion perception network
fMRI	Functional magnetic resonance imaging
HFA	High-functioning autism
SCS	Self-Construal-Scale
TD	Typically developed
ToM	Theory of mind
VC	Virtual characters

List of Experimental Studies

Published:

Study 1	**Krämer, K.**, Bente, G., Luo, S., Pfeiffer, U. J., Han, S., & Vogeley, K. (2013). Influence of Ethnic Group-Membership and Gaze Direction on the Perception of Emotions. A Cross-Cultural Study between Germany and China. *PLoS ONE*, *8*(6), e66335.
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Study 2	**Krämer, K.**, Bente, G., Kuzmanovic, B., Barisic, I., Pfeiffer, U. J., Georgescu, A. L., & Vogeley, K. (2014). Neural correlates of emotion perception depending on culture and gaze direction. *Culture and Brain*, 1–25. doi:10.1007/s40167-014-0013-9
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1. General Introduction

The ability to perceive and accurately interpret dynamic nonverbal cues is an important aspect of social cognition, as it enables humans to understand and successfully interact with others (Birdwhistell, 2011; Burgoon, 1994). Interestingly, a variety of factors influences the perception of dynamic nonverbal cues. During the perception of dynamic facial expressions, for example, the cultural background as well as the gaze direction of the person who displays the emotion are relevant (Wieser & Brosch, 2012). Furthermore, deficits in social cognition, characteristic of neurodevelopmental disorders like high-functioning autism (HFA), can lead to impairments in the perception of dynamic nonverbal cues (Baron-Cohen, Leslie, & Frith, 1985).

1.1 The Perception of Facial Emotional Expressions

Facial emotional expressions have a strong communicative and social function in human interactions. They provide important nonverbal cues that enable us to better understand others (Bavelas, Black, Lemery, & Mullett, 1986; Frith, 2009). Over the past years, several neuroimaging studies have investigated the neural correlates of emotion perception (Barrett, Mesquita, Ochsner, & Gross, 2007; Murphy, Nimmo-Smith, & Lawrence, 2003; Phan, Wager, Taylor, & Liberzon, 2002). A recent meta-analysis by Lindquist et al. (2012) found no evidence for the perception of certain emotions being consistently and specifically linked to the activation in distinct brain regions. Rather a widely spread network of brain regions is activated during the perception and interpretation of a variety of different emotion categories (emotion perception network; EPN; see Fig. 1). The amygdala, which has often been shown to respond to stimuli that are novel or salient to participants (Adolphs, 2009; Herry et al., 2007), and the anterior insula, which is involved in processing affective states (Craig, 2002; Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004), are central components of the EPN. Also, regions that are associated with high-level cognitive reasoning are activated when emotions are processed. Among these regions are the dorsomedial prefrontal cortex (dmPFC), the ventromedial prefrontal corted (vmPFC), and the posterior cingulated cortex (PCC) (Mitchell, 2009; Schacter, Addis, & Buckner, 2007; Vincent et al., 2006). Finally, as emotion perception is often investigated using visual stimuli, the visual cortex and the face processing network (including the inferior frontal gyrus (IFG), the dorsolateral prefrontal cortex (dlPFC), the thalamus, the fusiform gyrus (FG), and the superior temporal sulcus (STS)) are typically activated during emotion perception (Johnson, 2005; Kober et al., 2008; Wieser & Brosch, 2012).

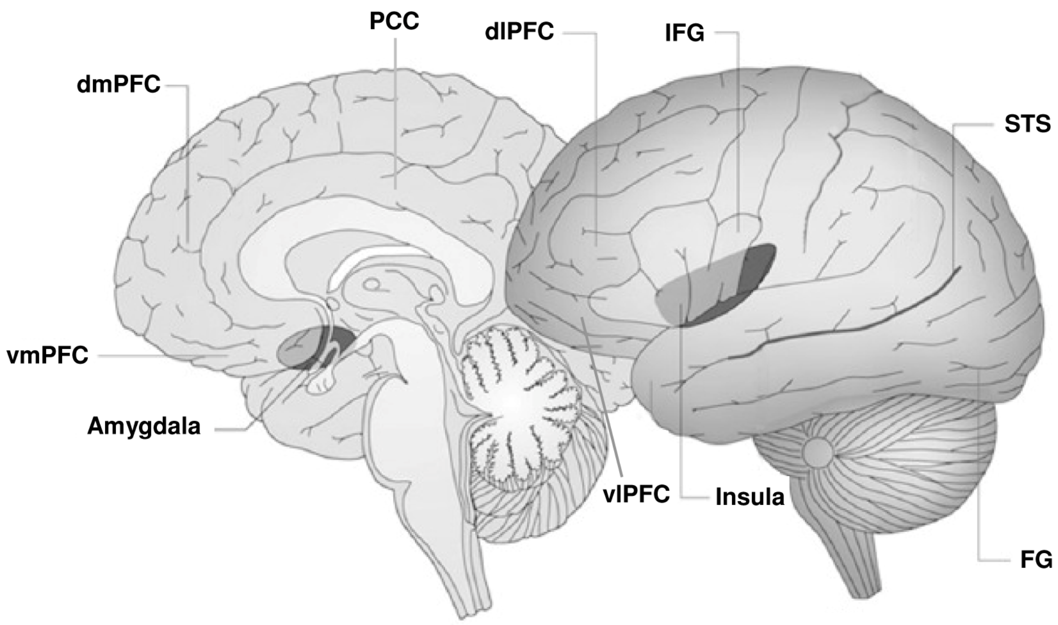

Figure 1. Emotion Perception Network (EPN). Depicted are the key regions involved in emotion processing in a medial and lateral view of the brain. See text for details and abbreviations (adapted from Blakemore, 2008).

Research has shown that the way emotional facial expressions are perceived highly depends on the dynamic characteristics of the stimulus material used, meaning on whether the emotions are presented dynamically in video sequences or statically with pictures (Wieser & Brosch, 2012). Several studies indicate that dynamic emotional expressions compared to static emotional expressions do not only offer an advantage in the intensity evaluation and recognition of emotions (Biele & Grabowska, 2006; Recio, Sommer, & Schacht, 2011), but also increase participants' facial reactions (measured with electromyography; EMG) to emotional expressions (Rymarczyk, Biele, Grabowska, & Majczynski, 2011; Weyers, Mühlberger, Hefele, & Pauli, 2006). Findings from functional magnetic resonance imaging (fMRI) studies further demonstrate that more widespread activation can be found in the EPN in response to dynamic compared to static facial expressions (Trautmann, Fehr, & Herrmann, 2009).

Finally, the way emotions are perceived depends on the situational context in which they are expressed (Wieser & Brosch, 2012). This situational context consists of a variety of different factors, such as characteristics of the emotion-encoder (i.e., the person who expresses the emotion), the emotion-decoder (i.e., the person who perceives the emotion), and the physical environment. Among these factors, two dynamic nonverbal cues influence emotion perception: i) The gaze direction of the emotion-encoder and ii) the cultural background of both the emotion-encoder and decoder. The gaze direction of the emotion-encoder provides an important social signal that offers crucial information for the interpretation of behavioural intentions conveyed by emotional expressions (Adams & Kleck, 2003). The cultural background of the emotion-encoder and decoder influence emotion perception, as they determine the emotion-encoder's feeling of belonging to the same ("cultural in-group") or a different ("cultural out-group") cultural group (Brown, Bradley, & Lang, 2006). Over the past years, the individual effects of gaze direction and culture on emotion perception have been investigated in a variety of studies (Adams & Kleck, 2003; Hess, Blairy, & Kleck, 2000; Schilbach et al., 2006). However, according to Wieser and Brosch (2012) these factors are interdependent which requires contemporary research on emotion perception to address the interactions between these factors.

1.2 The Perception of Animacy in Dynamic Objects

Animacy perception is defined as the perception of other entities as intentional, mindful agents (Santos, David, Bente, & Vogeley, 2008). It is a crucial ability for social cognitive processes, such as Theory of Mind (ToM), which involves inferences about mental states of others. Interestingly, this ability is not restricted to the perception of dynamic nonverbal cues that are displayed by humanoid appearances: Observers are able to perceive even non-biological geometric objects as acting intentional and having a mind by identifying specific intentions and goals in dynamic movement patterns (Heider & Simmel, 1944). Thus, they judge social interactions and attribute intentions, thoughts and desires to moving entities they perceive as animated by making use of their implicit knowledge of social contingencies (Santos et al., 2010, 2008; Scholl & Tremoulet, 2000).

However, this ability seems to be impaired in HFA. Individuals with HFA show specific cognitive deficits relating to the representation of mental states of others (Baron-Cohen, 1997). Especially, the spontaneous, intuitive attribution of and reaction to mental states seems to be impaired, while the analytic reasoning is intact (Klin, 2000; Senju, Southgate, White, & Frith, 2009). In animacy perception tasks, this results in a specifically impaired social but not physical attribution (Klin & Jones, 2006), with less frequent spontaneous interpretations of animated stimuli in terms of social and mentalistic aspects (Klin, 2000).

Taken together, it becomes evident that investigating the perception of animacy in dynamic objects not only enables a better specification of the mechanisms underlying social cognition in typically developed (TD) individuals, but also promotes a better understanding of neurodevelopmental disorders like HFA.

1.3 Methodological Approaches to the Investigation of Dynamic Nonverbal Cues

Over the last years, a great amount of research has shown that virtual characters (VC) provide a useful research tool to investigate the perception of dynamic nonverbal cues (Vogeley & Bente, 2010). Apart from the fact that their nonverbal behaviour and their outward appearance can be controlled and varied systematically (Dyck et al., 2008), several studies demonstrated that the nonverbal behaviour of VCs is perceived in much the same way as the nonverbal behaviour of real human beings (Bente, Petersen, Krämer, & De Ruiter, 2001; Garau, Slater, Pertaub, & Razzaque, 2005). In addition, research in so-called shared virtual environments has repeatedly shown that interactions with VCs follow the same social norms as social interactions with real persons (Bailenson, Blascovich, Beall, & Loomis, 2003; Blascovich et al., 2002; Ouellette, Chagnon, & Faubert, 2009). Due to this high degree of ecological validity, a great number of studies used VCs to study human behaviour in interactions over the last years (Bailenson & Yee, 2005; Bente, Leuschner, Al Issa, & Blascovich, 2010; Georgescu et al., 2013; Pfeiffer, Timmermans, Bente, Vogeley, & Schilbach, 2011; Schönbrodt & Asendorpf, 2012). Most importantly for **Study 1** and **Study 2** of the present thesis, previous research on the perception of emotions expressed by VCs has shown that virtual and natural emotional expressions are recognised to a comparable degree (Dyck et al., 2008). Interestingly, not only the passive detection of emotions is comparable to real-life encounters. Also, the effect of emotional contagion occurs in interactions with VCs: Participants show facial mimicry in reaction to VCs' emotional expressions (measured with EMG) (Likowski, Mühlberger, Seibt, Pauli, & Weyers, 2008; Schilbach, Eickhoff, Mojzisch, & Vogeley, 2008; Schrammel, Pannasch, Graupner, Mojzisch, & Velichkovsky, 2009). Thus, the application of VCs as a research tool is particularly suited for the investigation of emotions, as facial expressions of VCs provide well-controlled, realistic and dynamic stimuli (Dyck et al., 2008).

In **Study 2** of the present thesis, fMRI was used to measure whole brain neural correlates of cognitive processes in addition to evaluative behavioural judgement tasks which targeted explicit attitudes towards the stimulus material (**Study 1**, **Study 2**, and **Study 3**). FMRI is a hemodynamic-metabolic method for non-invasively and indirectly measuring brain activity. By making use of the blood oxygenation level-dependent (BOLD) effect (Heeger & Ress, 2002), neural correlates of cognitive processes are measured in a strong static magnet field combined with radio wave pulses and gradients. Cognitive processing is associated with an increase in neuronal firing rates which leads to increased metabolic requirements for the neurons. As a result of this, the cerebral blood volume and blood flow change in the local network of blood vessels. This leads to a decrease in deoxyhaemoglobin compared to oxyhaemoglobin in the venous pool. Deoxyhaemoglobin and oxyhaemoglobin have different magnetic properties. Deoxyhaemoglobin is paramagnetic and introduces an inhomogeneity into the nearby magnetic field, whereas oxyhaemoglobin is weakly diamagnetic and has little effect. Hence, a decrease in deoxyhaemoglobin causes an increase in image intensity (Heeger & Ress, 2002). Although the hemodynamic-metabolic details are not yet fully understood, the validity of the BOLD signal has been confirmed by relating it to direct neurophysiological intracortical recordings of neural activity (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001; Raichle & Mintun, 2006).

In **Study 3** of the present thesis, the perception of animacy induced by dynamic nonverbal cues of geometric objects was studied in TD and HFA participants. Heider and Simmel (1944) were the fist researchers to show that humans are able to perceive moving entities as animated beings, even when these entities are not human-shaped but geometric objects. They conducted an experimental paradigm in which participants had to watch video sequences of moving geometric objects. In these video sequences, the geometric objects moved as if following and reacting to one another. Participants perceived these interactive movement patterns as social encounters and ascribed human qualities to these non-biological objects. This fundamental work inspired many to use similar paradigms for the investigation of animacy perception. In line with this, Santos et al. (2008) developed a paradigm that further investigated the specific kinematic factors that influence animacy perception. They found that animacy perception increased with increasing complexity of interaction between the dynamic geometric objects (approach and response behaviour). Furthermore, the results suggested that their experimental paradigm would be sensitive enough to parametrically modulate animacy perception in typical and psychopathological development as it induces a continuous graduate increase of animacy perception. Thus, in **Study 3** of the present thesis, we decided to use the paradigm of Santos et al. (2008) to study the perception of animacy induced by geometric objects' movement patterns in TD and HFA participants.

1.4 Aims of the Present Thesis

The studies included in the present thesis aimed at investigating the perception of dynamic nonverbal cues in two major domains of social cognition: The perception of emotions across cultures and the perception of animacy in HFA. In particular, **Study 1** focused on the investigation of cultural differences in emotion perception depending on culture and gaze direction between Chinese and German participants. In **Study 2**, the previously implemented research paradigm was used to uncover the effect of culture and gaze direction on the neural correlates of emotion perception in German participants using fMRI. Finally in **Study 3**, disturbances in social cognition during the perception of dynamic nonverbal cues were investigated. Here, HFA and TD participants' animacy perception of geometric objects that moved with varying motion complexity was compared. The present thesis gives an overview of research questions and findings of all studies. Also, theoretical backgrounds and arising conclusions are interrelated to each other.

2. Study 1: Influence of Culture and Gaze Direction on Emotion Perception: Behavioural Findings

2.1 Theoretical Background

2.1.1 Influence of Cultural Group-Membership on Emotion Perception

Previous research has shown that while emotions can be accurately and consistently decoded across different cultures (Ekman & Friesen, 1971; Mesquita & Frijda, 1992), nonverbal dialects and accents in facial expressions of emotions exist. This enables people to perform better at decoding emotions expressed by members of their cultural in-group compared to emotions expressed by members of a cultural out-group (Elfenbein & Ambady, 2002; Elfenbein, 2013; Jack, Garrod, Yu, Caldara, & Schyns, 2012; Marsh, Elfenbein, & Ambady, 2003).

Brown et al. (2006) investigated participants' emotional responses to pictures of cultural in-group and out-group members which varied in pleasantness. Their results showed that pictures of cultural in-group members evoked greater pleasure and displeasure and thus more extreme ratings compared to pictures of cultural out-group members. According to the authors, this indicates that in-group dynamics may exert a greater influence on affective reactions than out-group dynamics. Also, the cultural background of emotion-encoders and decoders has been shown to have an effect on the perception of intentions conveyed by emotional expressions. Hess et al. (2000) investigated emotion-encoders ratings of dominance and affiliation based on cultural stereotypes. They expected that the perceived likelihood of an expression to be shown by members of a specific cultural group would influence dominance and affiliation ratings. Their results supported these hypotheses: North Americans were rated as more dominant and more likely to show anger than Asians. Furthermore, happiness displays by Asians were rated as more affiliative than happiness displays by North Americans. Accordingly, Asians were rated as more likely to show happiness than North Americans. Thus, the likelihood of the emotional display predicted dominance and affiliation displays.

2.1.2 Influence of Gaze Direction on Emotion Perception

Gaze direction is an important nonverbal cue in social interactions and communication (Cary, 1978). By indicating a person's focus of attention (Mason, Tatkow, & Macrae, 2005), direct gaze can for instance indicate a potential social interaction as it signals a perceiver that she/he has been noticed by another person (Senju & Johnson, 2009). In line with this, Schilbach et al. (2006) showed that gaze direction influences the perceived engagement with an interaction partner. In their study, participants felt more engaged with a VC when they were directly gazed at as compared to when they merely observed a VC showing averted gaze towards another person.

Furthermore, gaze direction has been shown to facilitate the recognition of emotions. Adams and Kleck (2003) found that approach-orientated emotions like anger and happiness were recognised more quickly and more accurately when expressed with direct compared to averted gaze. According to the authors, these results suggest that apart from providing an important social signal, gaze direction additionally offers contextual information that is critical for the interpretation of behavioural intentions conveyed by dynamic emotional expressions.

2.1.3 Interaction Effect of Culture and Gaze Direction

Previous research has shown that the way emotions are perceived depends on the situational context in which they are expressed (see 1.1) (Wieser & Brosch, 2012). This situational context is constituted by different factors, such as characteristics of the emotion-encoder (e.g. gaze direction and expression dynamics), the emotion-decoder (e.g. cultural background), and the physical environment. As argued above, research has repeatedly shown the individual influences culture and gaze direction exert on emotion perception (see 2.1.1 and 2.1.2). However, according to Wieser and Brosch (2012) these factors are interdependent which requires contemporary research on emotion perception to address the interaction between these factors.

Hence, we decided to investigate the combined influence of culture and gaze direction on emotion perception in **Study 1**. We argue that the investigation of these two factors provides a great approach to study critical mechanisms of social cognition, as both factors are nonverbal and can be presented in a combined stimulus set.

2.2 Experimental Design and Hypotheses

Study 1 (Krämer et al., 2013) aimed at investigating the combined influence of culture and gaze direction on emotion perception. We investigated participants from the Eastern (China) and the Western (Germany) culture, as these cultures are known to differ in cultural constructs such as individualism and collectivism (Hofstede, 1984, 2001; Markus & Kitayama, 1991).

We designed a four-factorial experimental paradigm in which we varied the factors (i) *VC's culture* (Asian versus European), (ii) *gaze direction* (direct versus averted), (iii) *emotion* (happiness versus anger), and (iv) *participant's culture* (Chinese versus German) (see Fig. 2). The software package FaceGen (© Singular Inversions Inc., Toronto, Canada, 2012) was used to create 20 three-dimensional (3D) Asian-looking VCs and 20 3D European-looking VCs from photographs of Chinese and German individuals. Further, 3-second long animations of the VCs' expressing happiness and anger were created using the virtual reality software Vizard (© WorldViz Inc., Santa Barbara, USA, 2012). Consequently, the stimulus material of **Study 1** consisted of short video sequences showing Asian-looking and European-looking VCs that expressed happiness and anger with direct and averted gaze. After each video sequence, a group of 40 Chinese participants (20 female; mean age 22.38 ± 2.17 years) born and raised in China, and a group of 40 German participants (20 female; mean age 23.93 ± 4.74 years) born and raised in Germany had to rate the perceived valence of the emotional expression on a four-point scale (positive – rather positive – rather negative – negative). Additionally, we measured the cultural constructs of individualism and collectivism using Singeli's Self-Construal-Scale (SCS) (1994). Results indicated that Chinese participants scored higher than German participants on the subscale measuring collectivism, $t(1, 78) = 5.696$, $p = .000$. In contrast, German participants scored higher than Chinese participants on the subscale measuring individualism, $t(1, 78) = 3.159$, $p = .002$.

We hypothesized that the valence appraisal of emotions is influenced both by the participants' and the VCs' cultural group-membership. Specifically, we hypothesized that emotions are rated more extremely when the participant and the VC are members of the same cultural group (Brown et al., 2006). Additionally, we expected participants of both cultural groups to rate the valence of emotions more extremely when displayed in combination with direct gaze as compared to averted gaze (Adams & Kleck, 2003). Finally, we hypothesized an interaction between culture and gaze direction, such that the effect of gaze direction on emotion perception would be more pronounced when the participant and the VC belonged to the same cultural group.

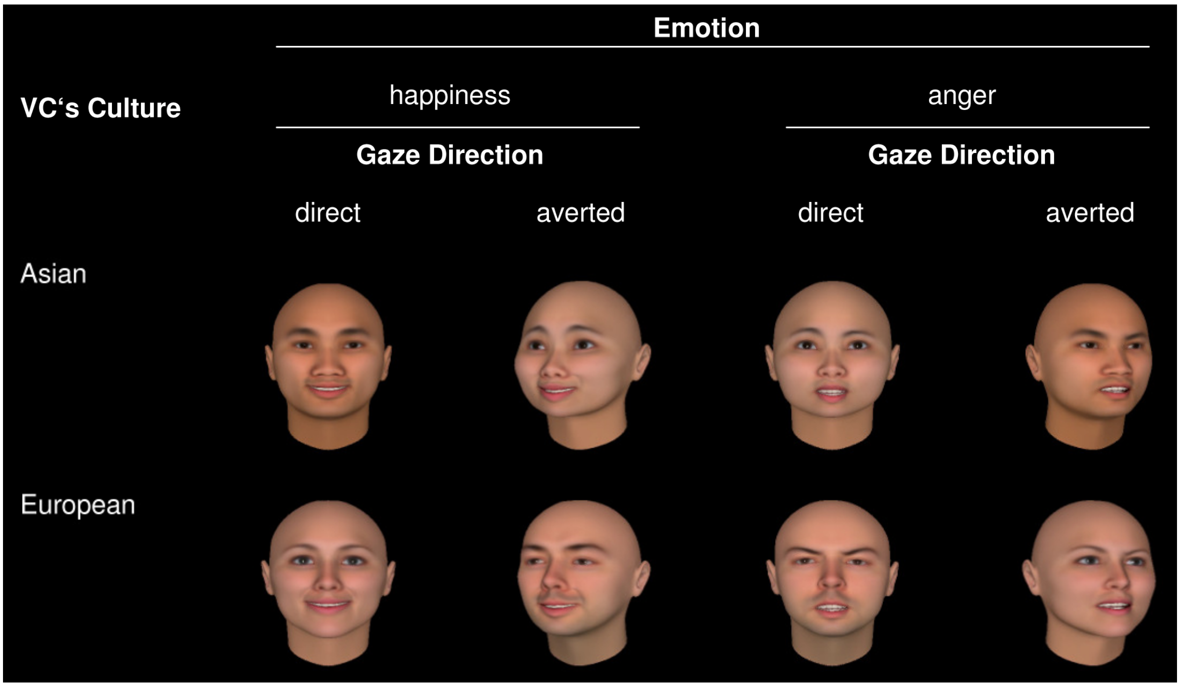

Figure 2. Experimental design and stimuli of **Study 1** with the factors *VC's culture*, *gaze direction*, and *emotion*. The between-subject variable is *participant's culture*. Participants' task was to watch the animations and rate the perceived valence of each emotion on a 4-point scale.

2.3 Findings and Conclusions

For **Study 1**, a mixed analysis of variance (ANOVA) with the between-group factor *participant's culture* and the three repeated-measures variables *VC's culture*, *gaze direction* and *emotion* was conducted using IBM SPSS Statistics 20 (SPSS Inc., Chicago, IL, 2011). Pairwise comparisons (Bonferroni-corrected) were computed to break down interaction effects (Field, 2009). Analyses revealed a significant interaction effect of *gaze direction*, *participant's culture*, *VC's culture*, and *emotion*, $F(1, 78) = 4.923$, $p = .029$, $r = .244$ (see Fig. 3a). Pairwise comparisons showed that Germans assessed *Asian anger direct* as more negative than *Asian anger averted* ($F(1, 78) = 1.717$, $p = .007$, $r = .147$). Additionally, Germans assessed *Asian happiness direct* as more positive than *Asian happiness averted* ($F(1, 78) = 8.610$, $p = .004$, $r = .315$). Interestingly, for Germans there was no difference in the valence appraisal of *European anger direct* compared to *European anger averted* and *European happiness direct* compared to *European happiness averted.* Concerning Chinese participants, results showed that they rated

European anger direct as more negative than *European anger averted* ($F(1, 78) = 4.963$, $p = .029$, $r = .245$) and *European happiness direct* as more positive than *European happiness averted* ($F(1, 78) = 12.154$, $p = .001$, $r = .367$). Furthermore, Chinese showed no difference in the valence appraisal between *Asian anger direct* and *Asian anger averted*. Interestingly, Chinese assessed *Asian happiness direct* more positively than *Asian happiness averted* ($F(1, 78) = 8.809$, $p = .004$, $r = .319$). In order to further investigate whether participants' SCS indices were related to the behavioural effects described above, correlation analyses were conducted. There was a significant relationship between *participants' SCS indices* and the assessment of *Asian happiness direct*, $r = .147$, $p = .03$: The more positive the SCS index of a participant was (i.e. the more agreement she/he showed for collectivistic items), the more positive she/he assessed *Asian happiness direct*. However, no other correlations of *participants' SCS indices* with the behavioural effects were significant. Overall, these results indicate that except for Chinese assessing *Asian happiness*, the intensity perception of an emotion did not depend on the emotion-encoder's gaze direction when she/he belonged to the cultural in-group of the emotion-decoder. However, when the emotion-encoder belonged to the cultural out-group of the emotion-decoder, the intensity perception of an emotion depended on her/his gaze direction.

Moreover, the significant four-way interaction between *participant's culture*, *VC's culture, gaze direction*, and *emotion* was further examined in order to investigate the influence of the VC's culture on the emotion appraisal of Germans and Chinese. Simple comparisons did not reveal any differences in the valence appraisal between Germans and Chinese when the VCs displayed an emotion while averting their gaze towards another person. Therefore, the results presented below only refer to VCs gazing directly at the participants (see Fig. 3b). There was no significant difference between Chinese and Germans in the appraisal of *European anger direct* ($F(1, 78) = 3.095$, $p = .082$). However, a tendency could be observed that Chinese assessed anger expressed by European VCs more negatively than Germans. A significant difference between Chinese and Germans in the appraisal of *European happiness direct* was found ($F(1, 78) = 4.723$, $p = .033$, $r = .239$): Chinese assessed happiness expressed by European VCs more positively than Germans. Furthermore, there was a significant difference between Chinese and Germans in the appraisal of *Asian anger direct* ($F(1, 78) = 4.288$, $p = .042$, $r = .228$). Germans rated anger expressed by Asian VCs more negatively than Chinese. Finally, we found no difference between Chinese and Germans in the appraisal of *Asian happiness direct*.

In sum, in **Study 1** we investigated the interaction between cultural group-membership and gaze direction on the perception of emotional expressions. Our results revealed that two factors which are known to have a considerable influence on emotion perception interact in their combined influence. Although previous research suggested that gaze direction influences emotion perception such that emotions are perceived as more extreme when expressed with direct gaze (Adams & Kleck, 2003; Schilbach et al., 2006), our findings indicate that culture influences this effect: Results show that the perceived intensity of an emotion expressed by cultural in-group members was in most cases independent of gaze direction, whereas gaze direction had an influence on the emotion perception of cultural out-group members. Furthermore, participants from the cultural out-group tended to perceive emotions as more pronounced than participants from the cultural in-group when they were directly gazed at. These findings suggest that gaze direction has a differential effect on cultural in-group and cultural out-group dynamics during emotion perception.

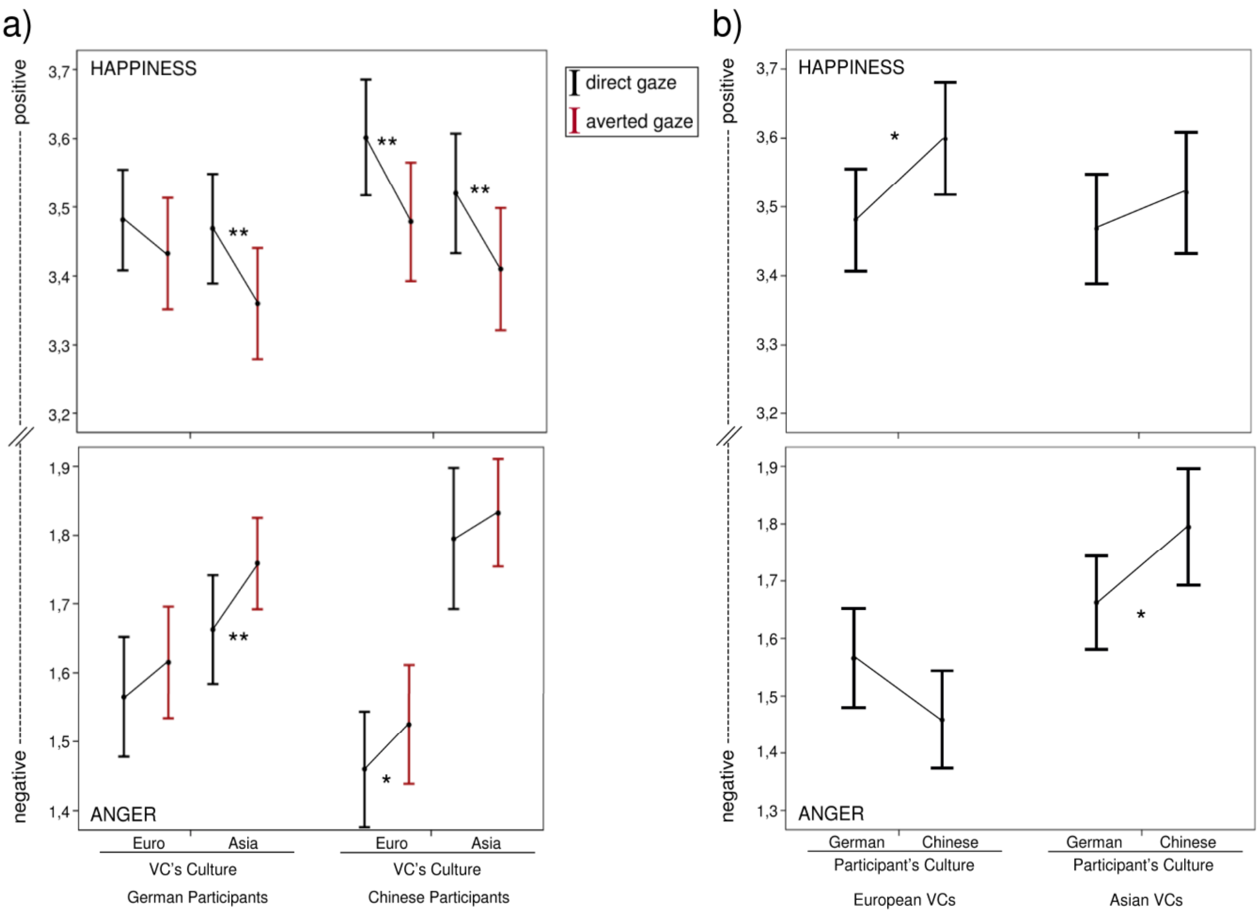

Figure 3. Results of **Study 1** investigating the interactive influence of culture and gaze direction on the valence perception of happiness and anger. a) Interaction effect of gaze direction, participant's culture, VC's culture, and emotion. b) Interaction effect of participant's culture, VC's culture, and emotion for direct gaze. Top panels show results for happiness, bottom panels show results for anger. Error bars indicate the 95% confidence interval. * *p*<.05; ** *p*<.01.

3. Study 2: Influence of Culture and Gaze Direction on Emotion Perception: Neural Findings

3.1 Theoretical Background

3.1.1 Neural Correlates of Emotion Perception Depending on Cultural Group-Membership

The influence the cultural group-membership of emotion-encoders and decoders exerts on emotion perception has been shown repeatedly in a variety of behavioural studies (Brown et al., 2006; Hess et al., 2000) (see 2.1.1). Over the past years, these behavioural studies have been accompanied by a large number of neuroimaging studies that investigated how the cultural background of emotion-encoders and decoders affects the neural substrates of emotion processing (for an overview see Ambady & Bharucha, 2009; Han & Northoff, 2008; Han et al., 2013; Kitayama & Uskul, 2011; Rule, Freeman, & Ambady, 2013).

Chiao et al. (2008), for instance, investigated the neural responses to faces of cultural in-group and out-group members expressing different emotions in Japanese and Caucasian participants. Their results revealed differential neural activation in the amygdala in response to fear expressed by cultural in-group compared to out-group members in both cultural groups: Japanese as well as Caucasian participants showed greater amygdala activation in response to viewing same-culture compared to other-culture fear expressions. According to Chiao et al. (2008), these results suggest that participants from both cultural groups interpreted fear displayed by cultural in-group members as a more salient signal of potential danger in comparison to fear displayed by cultural out-group members.

3.1.2 Neural Correlates of Emotion Perception Depending on Gaze Direction

Apart from the influence gaze direction exerts on the behavioural aspects of emotion perception (see 2.1.2), Schilbach et al. (2006) showed that the perception of being engaged with a VC as indicated through direct compared to averted gaze yielded enhanced neural activation in the dmPFC. The authors interpreted this as evidence for the involvement of the dmPFC in the detection of self-relevance indicated through direct gaze.

Furthermore, research with Caucasian (Adams, Gordon, Baird, Ambady, & Kleck, 2003; Hadjikhani, Hoge, Snyder, & de Gelder, 2008) as well as Asian participants (Sato, Yoshikawa, Kochiyama, & Matsumura, 2004) yielded further insights into how gaze direction influences the processing of different emotional expressions. In the case of anger, the amygdala showed more activation in response to anger expressed towards the emotion-decoder as compared to anger expressed away from the emotion-decoder (Hadjikhani et al., 2008; Sato et al., 2004). Additionally, in the case of fear, increased activity in response to fear expressed with direct compared to averted gaze was found in areas related to gaze processing (STS, intraparietal sulcus), face processing (FG, STS), fear processing (amygdala, hypothalamus), and motor preparation (premotor and motor cortices, superior parietal lobule; Hadjikhani et al., 2008). These results suggest that a distributed neural network integrates information provided by emotional expressions and gaze direction in order to compute implications for the emotion-decoder and adjust her/his behaviour accordingly.

3.1.3 Interaction Effect of Culture and Gaze Direction

As in the case of behavioural research, a wealth of neuroimaging studies have investigated the individual influences of culture and gaze direction on the neural correlates of emotion processing. Research on their combined influence, however, remains limited. To the best of our knowledge, there is only one neuroimaging study which directly assessed the combined influence of culture and gaze direction on the neural correlates of emotion processing (Adams et al., 2010). In this study, American and Japanese participants viewed rapid presentations of fear expressions shown by cultural in-group and out-group members with direct and averted gaze, while undergoing fMRI. Results showed differential neural activation in the EPN and in brain regions known to be involved in gaze processing in both American and Japanese participants: Fear expressed with direct gaze evoked greater responses for cultural out-group members in the respective brain areas, whereas fear expressed with averted gaze evoked greater responses for cultural in-group members in the respective brain areas.

However, the study of Adams et al. (2010) did not consider that depending on the valence of an emotion, culture and gaze direction can exert a differential influence on emotion perception (Krämer et al., 2013). Based on this, one could expect that also the influence of culture and gaze direction on the neural correlates of emotion processing might vary depending on the emotions' valence. Due to the fact that Adams et al. (2010) investigated the impact of culture and gaze direction only on one emotion that contains a negative valence (fear), no conclusions can be drawn for the influence of culture and gaze direction on the neural correlates of the perception of other emotions with different valences. Also, Adams et al. (2010) used static stimulus material which was shown to participants for only a short amount of time. Previous studies, however, indicated that dynamic nonverbal cues are ecologically more valid and thus more informative than static ones (see 1.1; Georgescu et al., 2013; Kuzmanovic et al., 2009; Schilbach et al., 2006; Wieser & Brosch, 2012).

Taken together, the results of previous research suggest that culture and gaze direction interact in their combined effect on the neural correlates of emotion processing. Furthermore, the valence of the expressed emotion seems to influence this interaction. Thus, in order to extend prior research and to uncover critical mechanisms underlying neural emotion processing, we decided to investigate the interactive influence of culture and gaze direction on the neural processing of happiness and anger in **Study 2**.

3.2 Experimental Design and Hypotheses

The aim of **Study 2** (Krämer et al., 2014) was to investigate the combined influence of culture and gaze direction on the neural processing of emotions with different valences. In this regard, we used the previously validated stimulus material of **Study 1** (see 2.2) which i) showed dynamic animations of facial expressions, ii) manipulated participants' perception of belonging either to the cultural in- or out-group of emotion-encoders, iii) systematically varied emotion-encoders' gaze direction, and iv) contained two distinct emotions differing in valence (Frijda, 1987). While undergoing fMRI, a group of 22 participants (11 female; mean age 24.5 ± 2.72 years) watched short video sequences showing dynamic facial expressions of happiness and anger, displayed by cultural in-group (Europeans) and out-group (Asians) members expressed with direct and averted gaze (see Fig. 2). After each video sequence, participants had to assess the perceived valence of the observed facial expressions on a four-point scale ranging from positive to negative (see Fig. 4a). For the purpose of generating stimulus material for the high-level baseline condition, 20 of the original animations were randomly chosen and converted into blurred videos via lowpass-filtering using a Matlab based algorithm (The Mathworks Inc., Natick, USA; see Fig. 1b). In these videos, only the shape and texture of the head and the face are recognisable, but no longer the expressed emotions or the VCs' cultural background (see Fig. 4b).

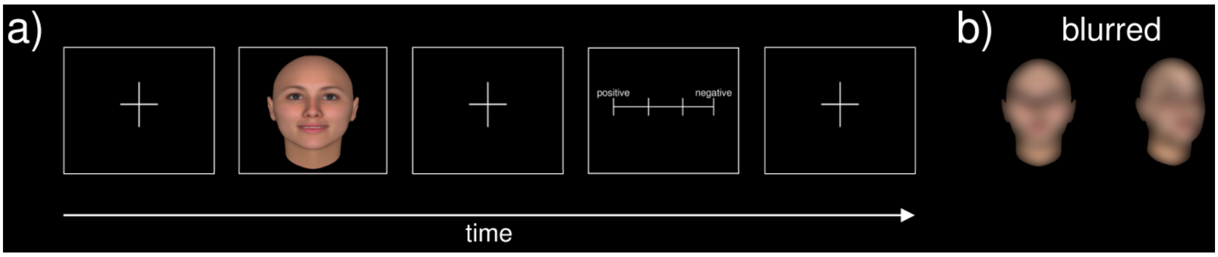

Figure 4. Trial structure and sample stimuli of **Study 2**. a) Example of an experimental trial: The participants' task was to watch each video sequence and rate the perceived valence of the expressed emotion on a 4-point scale. b) Sample frames extracted out of blurred videos which served as high-level base line.

We expected EPN activation to depend on both the cultural background and the gaze direction of the emotion-encoder (Chiao et al., 2008; Schilbach et al., 2006). In addition, the influence of culture and gaze direction was expected to differ for emotions with positive and negative valence (Krämer et al., 2013). With regard to anger, based on the findings of Adams et al. (2010) who investigated the interactive influence of culture and gaze direction on the neural processing of a negative emotion, we hypothesized that anger expressed with averted gaze would enhance EPN activation in response to cultural in-group members, whereas anger expressed with direct gaze would elicit stronger EPN activation in response to cultural out-group members. With regard to happiness, we expected the greatest neural response in the EPN for happiness expressed with direct gaze, because this combination of nonverbal signals conveys the greatest communicative intention and self-relevance (Schilbach et al., 2006). Moreover, its appetitive impact may be greater for cultural in-group than cultural out-group members.

3.3 Findings and Conclusions

Behavioural data of **Study 2** were analyzed using IBM SPSS Statistics 20 (SPSS Inc, Chicago, IL, 2011). A three-way repeated measures ANOVA with *culture*, *emotion*, and *gaze direction* as independent variables and the valence ratings as the dependent variable was conducted. We found a significant interaction effect of *culture* and *emotion*, $F(1, 20) = 8.687$, $p = .008$, $r = .304$ (see Fig. 5). Pairwise comparisons (Bonferroni-corrected) revealed that participants perceived *European anger* more negative than *Asian anger*. This is in line with previous findings which suggested that cultural stereotypes, such as the perceived enhanced likelihood for Caucasians to express more anger than Asians, have an influence on the perception of emotions (Hess et al., 2000).

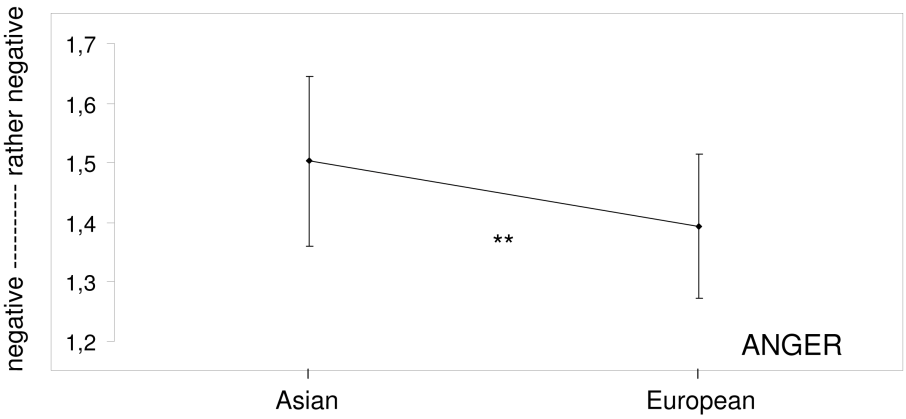

Figure 5. Behavioural results of **Study 2** showing the interaction effect of culture and emotion for anger perception. The scales on the y-axis indicate the mean of valence ratings of stimuli (1 = negative; 2 = rather negative). Error bars indicate the 95% confidence interval; ** $p < .01$.

Neural results indicated a differential influence of gaze direction on the processing of anger depending on the cultural background of the emotion-encoder. As hypothesised, results of anger processing indicated that when anger was expressed with averted gaze, more activation was found in the EPN in response to cultural in-group than out-group members, whereas when anger was expressed with direct gaze, more activation was found in areas of the EPN in response to cultural out-group than in-group members: FMRI analyses revealed greater activation in response to *European anger averted* compared to *Asian anger averted* in the right amygdala, a structure that has been shown to respond to perceptual stimuli that are salient to participants (Adolphs, 2009; Herry et al., 2007) and bilaterally in the putamen and the caudate nucleus (see Fig. 6a), two striatal structures associated with reward processing (Balleine, Delgado, & Hikosaka, 2007; Delgado, Locke, Stenger, & Fiez, 2003). The comparison of *Asian anger direct* compared to *European anger direct* yielded enhanced neural activation in two areas of the EPN, the dmPFC and the left dlPFC (see Fig. 6b). While the dlPFC has been shown to engage in a regulatory mechanism that controls implicit and potentially unwanted racial associations and racially biased responses in previous cross-cultural studies (Ito & Bartholow, 2009; Kubota, Banaji, & Phelps, 2012), Mitchell et al. (2005) could link dmPFC activation to mentalizing about dissimilar compared to similar others. Interestingly, similar activation patterns in the dmPFC and the left dlPFC were found in the comparison of *anger direct* compared to *anger averted* expressed by *Asian* relative to *European* VCs. FMRI analysis of this interaction effect further revealed activation in the PCC (see Fig. 6c), an area of the EPN that is involved in using prior experiences in order to decode and evaluate emotional expressions (Johnson et al., 2006; Ochsner et al., 2004).

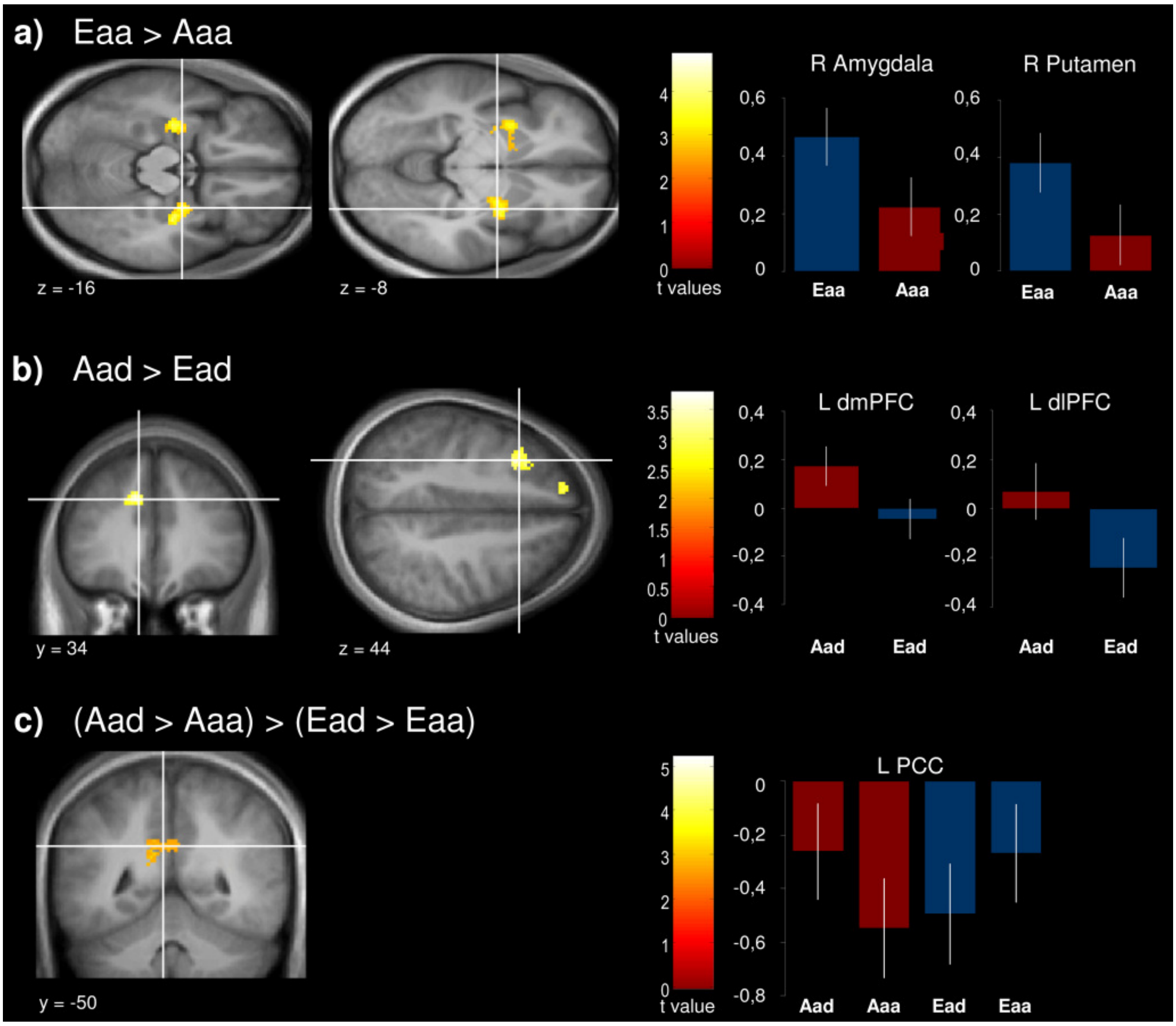

Figure 6. Neural results of **Study 2** investigating the effects of culture and gaze direction on the processing of anger. a) Differential neural activity for observing *European anger averted* compared to *Asian anger averted* (Eaa>Aaa). Plots illustrate corresponding contrast estimates obtained for the two stimulus categories for two different local maxima: right Amygdala (28, -8, -16), right Putamen (30, -2, -8); b) Differential neural activity for observing *Asian anger direct* compared to *European anger direct* (Aad>Ead). Plots illustrate corresponding contrast estimates obtained for the two stimulus categories for two different local maxima: left dmPFC (-12, 34, 34), left dlPFC (-32, 18, 44); c) Differential neural activity for observing *anger direct* compared to *anger averted* expressed by *Asian* compared to *European* VCs ((Aad>Aaa)>(Ead>Eaa)). Plots illustrate corresponding contrast estimates obtained for the four stimulus categories for local maxima of left PCC (-3, -50, 28); Error bars indicate the 90% confidence interval. The principally activated voxels are overlaid on the mean structural anatomic image of the 22 participants. p<.05, FWE-corrected for multiple comparisons at the cluster level; L = left hemisphere; R = right hemisphere; dmPFC = dorsomedial prefrontal cortex; dlPFC = dorsolateral prefrontal cortex; PCC = posterior cingulate cortex.

In sum, our results suggest that a direct threat (*anger direct*) was perceived as more salient when expressed by cultural out-group compared to in-group members, whereas an ambiguous threat (*anger averted*) was perceived as more salient when expressed by cultural in-group compared to out-group members.

Furthermore, in concordance with our hypothesis our results revealed that the influence of culture and gaze direction on the neural processing of happiness (an emotion with positive valence) differed from the neural processing of anger (an emotion with negative valence). The results of happiness processing indicated enhanced activation in a number of brain areas of the EPN when cultural in-group compared to out-group members expressed a positive emotion with direct gaze: The comparison of *European happiness direct* compared to *Asian happiness direct* yielded enhanced neural activation in several areas of the EPN, including the left IFG and the vmPFC (see Fig. 7a). In line with our findings, a greater recruitment of the IFG was found by Greer et al. (2012) in response to happiness expressed by cultural in-group members in European-American as well as African-American participants. The vmPFC has been linked to the experience of positive emotions (Winecoff et al., 2013) and mentalizing about faces participants' rated as similar to themselves compared to faces they rated as dissimilar to themselves (Mitchell et al., 2005). The comparison of *happiness direct* compared to *happiness averted* expressed by *European* relative to *Asian* VCs yielded similar activation patterns in the left IFG and the vmPFC. Interestingly, fMRI analysis of this interaction effect further revealed activation patterns in the left anterior insula (see Fig. 7b), an area that has been shown to be activated by positive associations in response to cultural in-group members (Beer et al., 2008). Overall, these results suggest that participants perceived a positive emotion expressed by cultural in-group members with direct gaze as a more salient cue than a positive emotion expressed by cultural out-group members with direct gaze.

Taken together, the results of **Study 2**, in which we investigated the combined influence of culture and gaze direction on the neural processing of anger and happiness, suggest a complex interplay between culture, gaze direction and the valence of the expressed emotion.

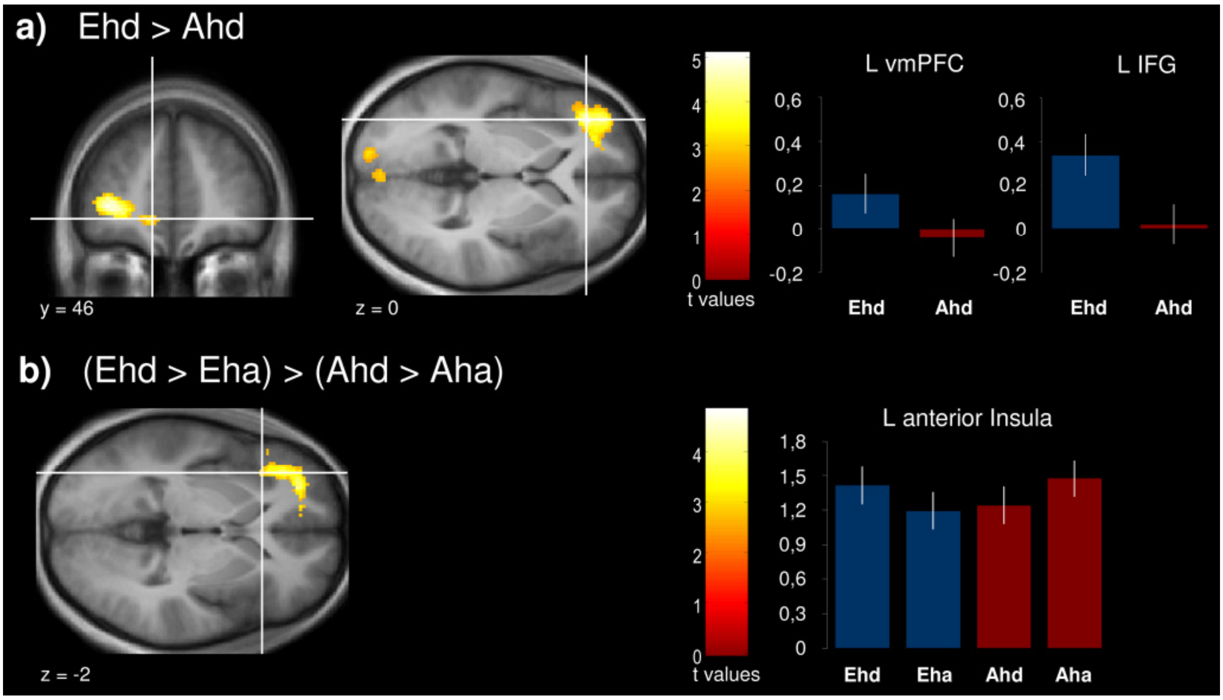

Figure 7. Neural results of **Study 2** investigating the effects of culture and gaze direction on the processing of happiness. a) Differential neural activity for observing *European happiness direct* compared to *Asian happiness direct* (Ehd>Ahd). Plots illustrate corresponding contrast estimates obtained for the two stimulus categories for two different local maxima: left vmPFC (-18, 46, -4), left IFG (-36, 40, 0). b) Differential neural activity for observing *happiness direct* compared to *happiness averted* expressed by *European* compared to *Asian* VCs ((Ehd>Eha)>(Ahd>Aha)). Plots illustrate corresponding contrast estimates obtained for the four stimulus categories for local maxima of left anterior insula (-36, 24, -2). Error bars indicate the 90% confidence interval. The principally activated voxels are overlaid on the mean structural anatomic image of the 22 participants: $p < .05$, cluster-level corrected; L = left hemisphere; R = right hemisphere; vmPFC = ventromedial prefrontal cortex; IFG = inferior frontal gyrus.

4. Study 3: Animacy Perception in High-Functioning Autism

4.1 Theoretical Background

4.1.1 The Perception of Dynamic Objects Induces Animacy

Biological motion is an important dynamic non-verbal cue that is relevant for the assessment of others' social communicative intentions (Bente et al., 2001; Chang & Troje, 2008; Georgescu et al., 2013; Thurman & Lu, 2013). Research using point-light displays as reduced body-representations can evoke a compelling impression of walking, running, or dancing (Dittrich, 1993; Johansson, 1973) and are sufficient for the perception of emotions (Clarke, Bradshaw, Field, Hampson, & Rose, 2005; Dittrich, Troscianko, Lea, & Morgan, 1996).

Intriguingly, our ability to attribute mental states to moving entities does not necessarily require a human-shaped object in motion (Berry, Misovich, Kean, & Baron, 1992; Castelli, Happé, Frith, & Frith, 2000; Heider & Simmel, 1944; Scholl & Tremoulet, 2000). In an early study, Heider and Simmel (1944) demonstrated that participants tended to attribute intentions, thoughts, and desires to non-biological geometric figures as they interpreted these figures as interacting with each other based on their dynamic, interactive motion patterns. Thus, animacy is experienced when we perceive other moving entities to be intentional and to possess a mind. Hence, for the perception of an entity as animated not only movements but also inferences about causes of movements are crucial (Dittrich & Lea, 1994; Gelman, Durgin, & Kaufman, 1995; Tremoulet & Feldman, 2006).

According to previous research, a number of dynamic cues can induce the interpretation of an entity as intentional and mindful and thereby enhance the perceived animacy. Among those cues is self-propelled motion, which enhances the impression of goal-directed action, as an object's movement is perceived as intentional when it begins to move without a perceivable external cause (Gergely & Csibra, 2003; Premack, 1990). Also, the degree of perceived interaction between entities (Dittrich & Lea, 1994; Heider & Simmel, 1944), which can for example be induced by an entity's approach and response behaviour (Santos et al., 2008), is essential for animacy perception.

4.1.2 Deficits of Animacy Perception in High-Functioning Autism

In TD individuals, the ability to perceive non-biological dynamic objects as animated entities arises early in infancy (Johnson, 2003; Luo & Baillargeon, 2005; Rakison & Poulin-Dubois, 2001; Shimizu & Johnson, 2004). Research, however, indicates that this ability is impaired in HFA patients, as they show less attributions of mental states (Abell, Happe, & Frith, 2000; Castelli, Frith, Happé, & Frith, 2002; Klin, 2000; Zwickel, White, Coniston, Senju, & Frith, 2011) as well as more frequent inappropriate mentalizing interpretations (Abell et al., 2000; Castelli et al., 2002; Klin, 2000) in response to moving geometric objects.

Interestingly, although HFA patients show deficits in social reasoning when social cues need to be intuitively attended to and processed, they are as capable of physical reasoning as TD participants are when physical stimulus properties need to be analyzed: While HFA participants were impaired in judging animations that indicated social phenomena (e.g., intentions or feelings) compared to TD participants, they interpreted moving geometric objects that indicated physical phenomena (e.g., a launching of a rocket into space from earth) comparably to TD participants (Klin & Jones, 2006). This indicates that HFA and TD participants are equally capable of integrative and global processing (Klin & Jones, 2006; Sebanz, Knoblich, Stumpf, & Prinz, 2005; Zwickel et al., 2011). However, HFA participants seem to be less attracted to social cues than TD participants are (Frith, 2004; Klin & Jones, 2006; Pelphrey, Morris, & McCarthy, 2005). This reduced intrinsic salience of social cues has been argued to underlie the observed impairments in spontaneous social responding in HFA (Baron-Cohen, Wheelwright, Robinson, & Woodbury-Smith, 2005; Klin, Jones, Schultz, & Volkmar, 2003; Kuzmanovic, Schilbach, Lehnhardt, Bente, & Vogeley, 2011).

4.2 Experimental Design and Hypotheses

Study 3 (Krämer et al., under review) aimed at investigating animacy perception in HFA and TD participants. We used an established paradigm developed by Santos et al. (2008) that has previously been used to study animacy perception (Kuzmanovic et al., 2014; Santos et al., 2010, 2008).

The stimulus material consisted of four categories of animations showing two spheres that moved in animacy-inducing motion patterns. All animations (duration of 2 – 5.7 sec) showed a red sphere in the foreground, and a green sphere passing from either side to the other in the background. The motion complexity of the spheres was systematically varied over the four stimulus categories by manipulating their approach and response behaviour in order to parametrically modulate the perceived animacy (see Fig. 8): The red sphere in the foreground either stayed static throughout the video sequence (no response), or moved towards the green sphere in the background (response). The green sphere on the other hand either moved from one side to the other without pausing (no approach), or paused in the middle of the screen and approached the red sphere in the foreground before leaving the scene (approach). Consequently, the systematic combinations of the spheres' approach and response behaviour resulted in four conditions with an increasing amount of motion complexity: (1) no approach and no response (A- R-), (2) no approach but a response (A- R+), (3) approach but no response (A+ R-), (4) approach and response (A+ R+).

In two successive runs, a group of 30 HFA participants (12 female; mean age 33.81 ± 9.33 years) and a group of 31 TD participants (12 female; mean age 30.81 ± 7.83 years) had to rate the subjectively perceived "person-likeness" on a four-point scale (physical – rather physical – rather person-like – person-like).

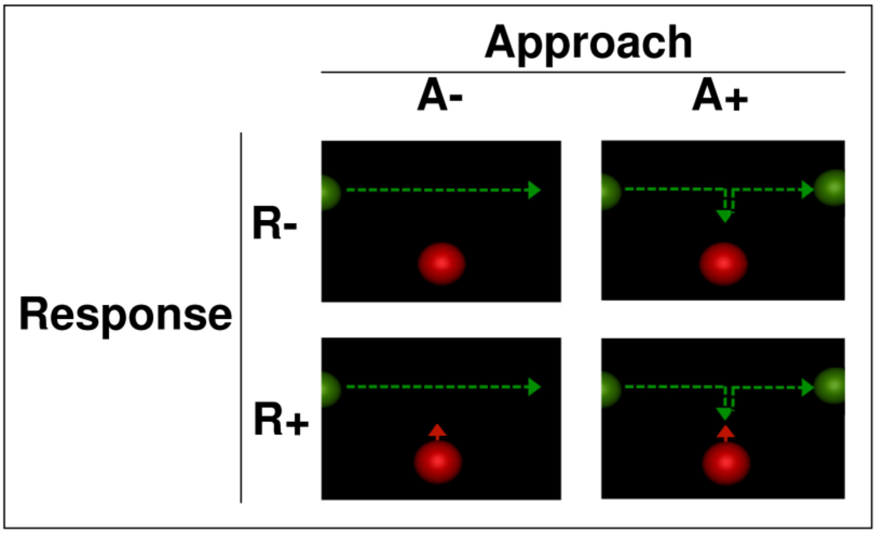

Figure 8. Experimental paradigm of **Study 3** with the factors *response* and *approach*. The approach and response behaviour of the two spheres was manipulated in order to vary the motion complexity of the stimulus material. The systematic combinations of the spheres' approach and response behaviour resulted in four conditions: (1) no approach and no response (A- R-), (2) no approach but a response (A- R+), (3) approach but no response (A+ R-), (4) approach and response (A+ R+). Participants' task was to watch the animations and rate the perceived "person-likeness" on a 4-point scale.

We expected HFA participants to perceive the animations as less animated compared to TD participants due to previous research revealing less frequent animacy attributions to animated shapes in spontaneous social responding in HFA (Castelli et al., 2002; Klin et al., 2003; Klin, 2000). Also, we hypothesized that HFA compared to TD participants would require more time to assess the animacy of the animations, as we assumed that the attribution of mental states to moving geometric objects is not done implicitly but explicitly in HFA (Congiu, Schlottmann, & Ray, 2010; Frith, 2004).

4.3 Findings and Conclusions

For **Study 3**, all data were analyzed using IBM SPSS Statistics 22 (SPSS Inc, Chicago, IL, 2013). In order to analyze whether HFA and TD participants differed in the frequency with which they chose either of the four possible response options ("physical", "rather physical", "rather person-like", "person-like"), a mixed ANOVA with the between-group factor *group,* the repeated-measures variable *motion complexity*, and the dependent variable *frequency of response-option* was conducted. Analyses showed that HFA and TD participants significantly differed in the frequency with which they chose either of the four possible response options ($F(3,59) = 6.174$, $p = .001$, $\omega^2 = .108$). Pairwise comparisons revealed that HFA participants rated more video sequences as "physical" compared to TD participants. In contrast to this, TD participants rated more video sequences as "person-like" compared to HFA participants. These findings are in line with previous research attesting less frequent animacy attributions to animated shapes in HFA (Abell et al., 2000; Castelli et al., 2002; Klin et al., 2003; Klin, 2000).

Furthermore, a mixed ANOVA with the between-group factor *group,* the repeated-measures variable *motion complexity*, and the dependent variable *animacy ratings* was conducted, to analyze the effect of increasing motion complexity on animacy ratings of HFA and TD participants. As hypothesized, we found a significant main effect of *group* ($F(1,59) = 14.838$, $p < .001$, $\omega^2 = .116$), suggesting that HFA participants rated the stimuli as less animated compared to TD participants. Although results showed no significant interaction effect between *group* and *motion complexity* ($F(3,59) = 0.429$, $p > .05$), pairwise comparisons revealed that HFA and TD participants significantly differed in their animacy ratings of the video sequences in all four conditions: HFA participants rated the video sequences that contained (1) no approach and no response behaviour, (2) no approach but a response behaviour, (3) approach but no response behaviour, and (4) approach and response behaviour as less person-like compared to TD participants (see Fig. 9).

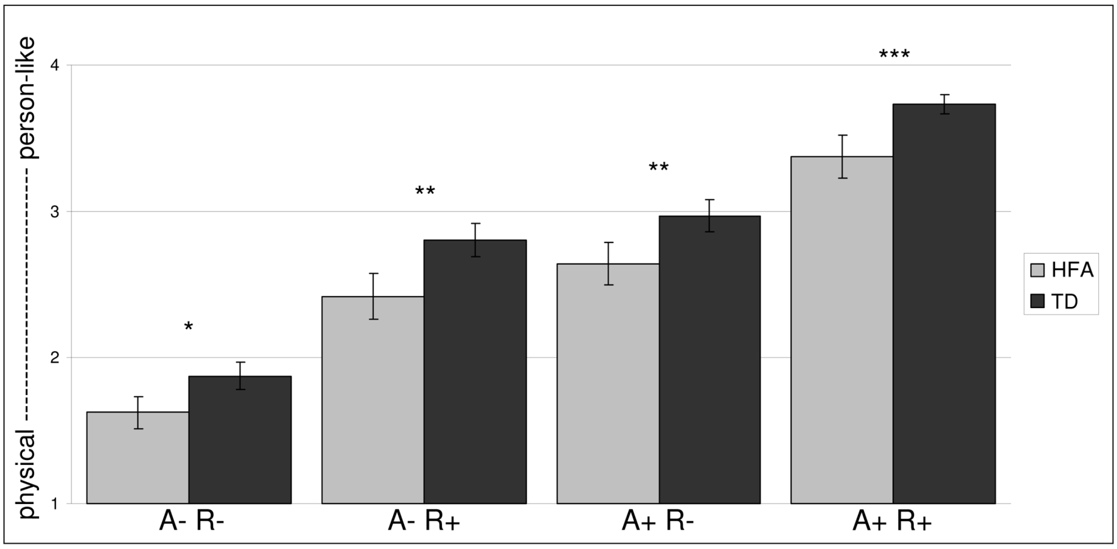

Figure 9. Results of **Study 3** investigating the interaction effect of group and motion complexity on animacy ratings. HFA = high-functioning autism participants; TD = typically developed participants; A- R- = no approach and no response; A- R+ = no approach and response; A+ R- = approach and no response; A+ R+ = approach and response; Error bars indicate the 95% confidence interval. * p < .05; ** p < .01; *** p < .001.

Finally, analyses of reaction times revealed that during the first experimental run HFA compared to TD participants showed longer reaction times in response to videos they rated as more animate ($F(3,59) = 6.097$, $p = .001$, $\omega^2 = .101$) (see Fig. 10). No reaction time differences between groups were found in response to videos they rated as more physical. Interestingly, during the second experimental run, we found no reaction time differences between HFA and TD participants ($F(3,59) = 0.080$, $p > .05$) (see Fig. 10), indicating a training effect for the HFA participants.

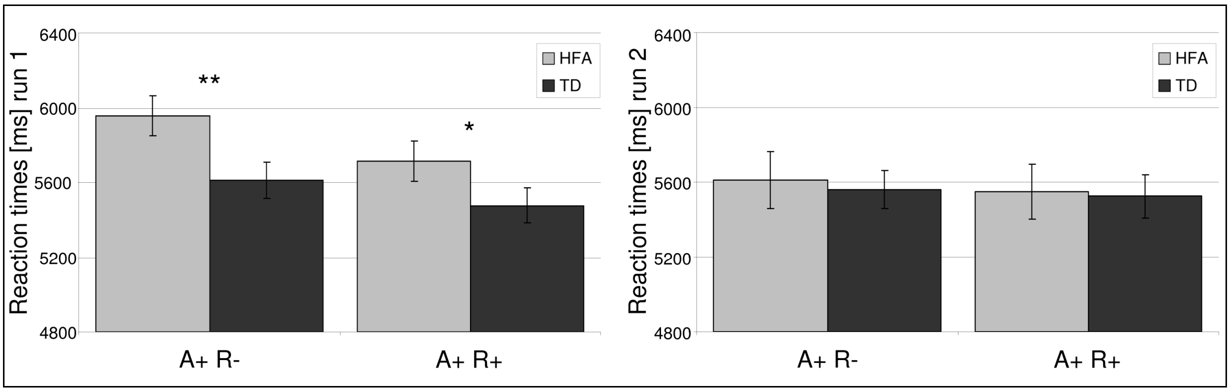

Figure 10. Results of **Study 3** investigating the interaction effect of group and motion complexity on reaction times of run 1 and run 2. HFA = high-functioning autism participants; TD = typically developed participants; A+ R- = approach and no response; A+ R+ = approach and response; Error bars indicate the 95% confidence interval. * p < .05; ** p < .01.

These results suggest that although HFA participants perceive and assess parametrically induced animacy comparably to TD participants, animacy perception might not be an a priori automatic cognitive process in HFA. Thus, the longer reaction times for the animacy assessments of HFA participants in the first experimental run might indicate that HFA participants can pass this task only at higher cognitive demands that arise from the ascription of humanness to non-biological geometric objects (Congiu et al., 2010; Frith, 2004; Rutherford, Pennington, & Rogers, 2006).

Taken together, the results of **Study 3** indicate that HFA participants compared to TD participants perceived the animations as less animated and showed longer reaction times in response to videos they rated as more animate in the first experimental run indicating an explicit versus implicit format of processing the given information. Interestingly, both groups showed a similar response pattern, as they perceived animations with an increasing amount of motion complexity as more animated ($F(3,59) = 130.889$, $p = .000$, $\omega^2 = .205$). This might indicate that, although the way HFA participants perceive parametrically induced animacy is comparable to TD participants, animacy perception might not be an automatic cognitive process in HFA, as it requires more time and does not reach the same intensity level compared to TD participants.

5. General Discussion

The findings of the three studies included in this thesis have already been discussed in the respective chapters (see 2.3, 3.3, 4.3). The following chapter aims at embedding the presented findings into a larger context of previous research. Furthermore, we will discuss how these findings extend current knowledge in the field of social cognitive research.

5.1 The Perception of Dynamic Emotional Cues across Cultures

In the general introduction (see 1), we argued that the ability to perceive and accurately interpret dynamic nonverbal cues is crucial for social cognition. It helps us to successfully interact with others (Birdwhistell, 2011; Burgoon, 1994). Especially, dynamic emotional cues have a strong communicative and social function, as the correct interpretation of these nonverbal cues enables us to better understand others in human interactions (Bavelas et al., 1986; Frith, 2009).

The way we perceive emotions is influenced by a variety of factors, such as the gaze direction of the emotion-encoder and the cultural background of the emotion-encoder and decoder. The behavioural results of **Study 1** indicate that during cross-cultural encounters, the gaze direction of the emotion-encoder had a differential effect on cultural in-group and out-group dynamics during emotion perception in cross-cultural interactions: During the perception of emotions expressed by cultural out-group members, direct gaze as compared to averted gaze increased and emphasized the valence perception of the emotions. However, during the perception of emotions expressed by cultural in-group members, in most cases gaze direction did not influence the emotions' intensity perception. Here, participants did not perceive emotions as more pronounced when they were expressed by cultural in-group members with direct compared to averted gaze. Only in the condition where Chinese participants assessed happiness expressed by Asian VCs, gaze direction had an influence: Our results indicate that Chinese participants assessed happiness expressed by Asian VCs with direct gaze as more positive than happiness expressed by Asian VCs with averted gaze. Research on differences in display rules between people from collectivistic and individualistic cultures might explain this deviating effect. Ekman and Friesen (1969) proposed that display rules help people to manage and adjust emotional expressions depending on situational demands and social circumstances.

It has been shown that there are differences in display rules between people from collectivistic and individualistic cultures (Markus & Kitayama, 1991; Matsumoto, 2006). According to Matsumoto (1990), people from collectivistic cultures show more positive emotional expressions towards cultural in-group members in direct interactions than people from individualistic cultures. In addition, he demonstrated that display rules predict persons' appropriateness ratings of the display of certain emotional expressions in social interactions. Based on these findings, one would expect Chinese participants to deem the expression of positive emotions towards cultural in-group members particularly appropriate in direct interactions. Furthermore, this might result in Chinese preferring the display of positive emotions towards cultural in-group members when expressed in combination with direct gaze as compared to averted gaze. This was, indeed, confirmed in the present study.

Overall, the behavioural results of **Study 1** demonstrate that the perception of dynamic emotional cues is more stable when the emotion-encoder and decoder belong to the same cultural group as compared to when they belong to different cultural groups. In the former case, the intensity perception of an emotion does not depend on the gaze direction of the emotion-encoder, whereas in the latter case, the intensity perception of an emotion decreases when the emotion-encoder does not show direct but averted gaze.

Study 2 aimed at extending the behavioural findings of **Study 1** by investigating the neural correlates of emotion processing during cross-cultural encounters. Apart from the factor gaze direction, which has already been shown to have an effect on emotion perception during cross-cultural interactions in **Study 1**, neural results of **Study 2** suggest that the influence culture exerts on the neural processing of dynamic emotional expressions varies according to the emotion's valence. In the case of happiness, fMRI results revealed that participants showed enhanced EPN activation in response to a positive emotion when it was expressed by cultural in-group compared to out-group members. This suggests that happiness expressed by cultural in-group members might be perceived as a more salient dynamic emotional cue than happiness expressed by cultural out-group members (Beer et al., 2008; Mitchell et al., 2005; Schilbach et al., 2006; Winecoff et al., 2013).

In the case of anger, the gaze direction of the emotion-encoder seems to further influence the neural processing of this particular emotional cue during cross-cultural interactions. Results showed that when anger was expressed with direct gaze, more EPN activation was found in response to cultural out-group compared to in-group members. We speculate that the evaluation of anger expressed by cultural out-group members (dissimilar others) induced increased high-level inferential cognitive processing such as mentalizing compared to the evaluation of anger expressed by cultural in-group members (similar others) (Mitchell et al., 2005). Also, we assume that the evaluation of a negative emotion and the regulation of intergroup behaviour elicited more activation in the EPN when participants observed cultural out-group compared to cultural in-group members (Cunningham et al., 2004; Ito & Bartholow, 2009; Kubota et al., 2012). Interestingly, when anger was expressed with averted gaze we found a different effect: More EPN activation was observed when cultural in-group compared to out-group members expressed anger with averted gaze. Enhanced activation, for example, was found in the amygdala. Chiao et al. (2008) observed greater amygdala activation in response to viewing fear expressed by cultural in-group compared to cultural out-group members in participants of two cultural groups. Furthermore, Adams et al. (2003) investigated the role of the amygdala in processing threat-related ambiguity by testing whether amygdala sensitivity to anger would differentially vary as a function of gaze direction. They found stronger amygdala responses for anger expressed with averted gaze (ambiguous threat) compared to anger expressed with direct gaze (clear threat). We conclude that the results of **Study 2** corroborate the findings of Chiao et al. (2008) and Adams et al. (2003) as our participants showed enhanced amygdala activation in response to what could be perceived as an ambiguous threat cue (*anger averted*) only when it was expressed by cultural in-group members. For cultural out-group members no such effect could be observed. This suggests that an ambiguous threat expressed by cultural in-group members might be perceived as a more salient dynamic emotional cue than an ambiguous threat expressed by cultural out-group members. Taken together, the results of anger processing suggest that a direct threat (*anger direct*) is perceived as more salient when expressed by cultural out-group compared to in-group members, whereas an ambiguous threat (*anger averted*) is perceived as more salient when expressed by cultural in-group compared to out-group members.

One major goal of this thesis was to investigate the social cognitive processes underlying the perception of dynamic (nonverbal) emotional cues during cross-cultural interactions (see 1.4). At a behavioural level (**Study 1**), in particular, the cultural background and the gaze direction of the emotion-encoder were shown to vary emotion perception, whereas at a neural level (**Study 2**) additionally the valence of the expressed emotion influenced the neural correlates of emotion perception. Taken together, the behavioural results of **Study 1** and the neural results of **Study 2** provided new evidence that in order to better understand the social cognitive processes underlying emotion perception, it is essential to investigate the interactive influence of a variety of factors that (individually) affect the perception of dynamic emotional expressions.

5.2 Deficits in Social Cognition: Animacy Perception in High-Functioning Autism

As discussed above (see 4.1.2), research indicates that individuals with HFA show a reduced intrinsic salience of social cues. This has been argued to underlie the observed impairments in the perception of animacy in moving geometric objects in HFA (Klin et al., 2003; Kuzmanovic et al., 2011). Intriguingly, in structured experimental settings, HFA participants are often able to correctly classify moving geometric objects as animated and thereby correctly interpret social stimuli (Congiu et al., 2010; U. Frith, 2004; Kuzmanovic et al., 2014). In order to further investigate animacy perception in HFA and to uncover underlying deficits in social cognition, we induced a parametric modulation of animacy perception in HFA and TD participants with the stimulus material we used in **Study 3**. Results show that by varying the stimulus' motion complexity we were able to induce a continuous, parametric increase of animacy perception (Kuzmanovic et al., 2014; Santos et al., 2010, 2008) and therefore provided a sensitive measure to investigate the ability to attribute mental states to animated geometric objects.

HFA participants showed similar response patterns compared to TD participants, as they perceived animations with an increasing amount of motion complexity as more animated. The groups, however, differed significantly in the intensity of their animacy ratings: HFA participants judged slower in the first experimental run and overall ascribed less animacy to the animations compared to TD participants. This indicates that although HFA participants perceived parametrically induced animacy comparably to TD participants, the basic cognitive processes that underlie animacy perception might differ between groups. Rutherford et al. (2006) came to similar conclusions after they found that under optimal experimental circumstances, autistic children were capable of identifying objects that moved as if animated. However, they took longer to learn how to identify such objects. Rutherford et al. (2006) argued that this was the case because HFA participants are not as interested in social information to the same amount as TD participants are (Dawson et al., 2004; Dawson, Meltzoff, Osterling, Rinaldi, & Brown, 1998; Mundy & Neal, 2000). Thus, the authors proposed the possibility that animacy perception might be preserved in autism, even if it is not used automatically. They speculated that the autistic children in their study learned to perceive animacy based on motion cues, but did not use the same brain regions or the same cognitive processes as the control group. The results of **Study 3** indicating longer reaction times for HFA compared to TD participants during the first but not the second experimental run as well as the results of a recent neuroimaging study by Kuzmanovic et al. (2014), support these speculations. Kuzmanovic et al. (2014), who used the same experimental paradigm as we did in **Study 3**, found that HFA and TD participants showed no behavioural differences in response to increasing motion complexity of stimuli. However, for TD compared to HFA participants, increasing animacy ratings more strongly correlated with activity in a neural network related to attribution of social meanings to ambiguous animated stimuli. These findings indicate that while HFA and TD participants showed similar response patterns in the attribution of increasing animacy to animated geometric objects at a behavioural level, neurally they did not respond to social cues intuitively and automatically but seemed to process this task by relying solely on physical stimulus analysis.

Taken together, in **Study 3** we employed a paradigm that not only induced a continuous graduate increase of animacy perception in TD participants, but for the first time confirmed that such a paradigm is sensitive enough to parametrically modulate animacy perception in HFA. Thereby, we were able to investigate disturbances in social cognitive processing during the perception of dynamic nonverbal cues in HFA that diminish the ability to attribute mental states to animated objects.

6. Conclusion

Our ability to perceive and accurately interpret dynamic nonverbal cues is essential for successful social interactions with others. In order to enhance our knowledge on the mechanisms that underlie the perception of dynamic nonverbal cues, the present thesis aimed at investigating this in two major domains of social cognition: The perception of emotions across cultures and the perception of animacy in HFA. First, we demonstrate that the way we behaviourally perceive and neurally process dynamic emotional cues in cross-cultural interactions is modulated by a variety of different factors (e.g. gaze direction, emotion's valence) which, apart from the individual influences they exert on emotion perception, interact in their combined influence on emotion perception. Second, the present work provides empirical evidence that while HFA participants are in general capable of perceiving animacy in moving geometric objects, they show a specific impairment in the automatic processing of animacy-inducing motion patterns compared to TD participants.

Taken together, the results of the present thesis suggest that studying the perception of dynamic nonverbal cues is in particular suitable for the investigation of social cognition in healthy and psychopathological contexts, as it enhances our understanding of its underlying behavioural and neural processes and provides an insight into how people navigate their social worlds.

7. References

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