Investigating the Dynamics of Nonverbal Communication:

Evidence from Neuroimaging in High-Functioning Autism and Typical Development

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List of Abbreviations

Abbreviation	**Meaning**
AON	Action observation network
ACC	Anterior cingulate cortex
ASD	Autism spectrum disorder
BOLD	Blood-oxygen level response
dlPFC	Dorsolateral prefrontal cortex
HFA	High-functioning autism
EBA	Extrastriate body area
EEG	Electroencephalography
FG	Fusiform gyrus
fMRI	Functional magnetic resonance imaging
IFG	Inferior frontal gyrus
IPL	Inferior parietal lobule
MEG	Magnetoencephalography
(v/d)mPFC	(Ventro-/Dorso-)medial prefrontal cortex
MT+/V5	Motion sensitive area
OFC	Orbitofrontal cortex
PCC	Posterior cingulated cortex
PCun	Precuneus
PLD	Point-light display
PMv/PMd	Ventral/dorsal premotor cortex
SMA	Supplementary motor area
SNN	Social neural network
(p)STS	(Posterior) superior temporal sulcus

ToM	Theory of Mind
TP	Temporal pole
TPJ	Temporo-parietal junction

List of Experimental Studies

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Study 1: Kuzmanovic, B., **Georgescu, A.L.**, Eickhoff, S.B., Shah, N.J., Bente, G. Fink, G.R., & Vogeley, K. (2009). Duration matters: dissociating neural correlates of detection and evaluation of social gaze. *NeuroImage, 46(4), 1154-1163.*

Contribution: A.L. Georgescu assisted in designing and testing the paradigm and stimulus material, as well as in collecting the data, commented on the manuscript.

Study 2: **Georgescu, A.L.**, Kuzmanovic, B., Schilbach, L., Tepest, R., Santos, N.S., Kulbida, R., Shah, N.J., Bente, G., Fink, G.R., & Vogeley K. (2013). Neural Correlates of "Social Gaze" Processing in High Functioning Autism Under Systematic Variation of Gaze Duration. *NeuroImage Clinical (accepted).*

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Study 4: Kuzmanovic, B., Schilbach, L., Georgescu, A. L., Kockler, H., Santos, N. S., Shah, J. N., Bente, G., Fink, G. R., & Vogeley. K. When seeing does not lead to feeling: Absent neural responses to increasing animacy judgments in high-functioning autism. *Social Neuroscience (under review).*

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1 General Introduction

It is widely accepted that nonverbal behaviors are an essential part of the human communication process: Burgoon (1994) summarizes that 60-65% of social meaning is communicated nonverbally. Therefore, the ability to accurately interpret other people's nonverbal behaviors is essential for successful social interactions, as it allows one to adjust one's own behavior to that of a social other. Indeed, throughout development, we become experts at attributing mental states and intentions to people based on nonverbal cues like facial expressions, hand gestures and bodily postures.

1.1 The Importance of Dynamic Aspects of Nonverbal Behavior in Communication

However, meaningful information is not only conveyed by static cues, but also by movements of the eyes, face, head or body. Thus, the spatiotemporal characteristics of perceived behavior also have an effect on how this information is processed (Birdwhistell, 1970). For example Krumhuber & Kappas (2005) found that temporal aspects of facial displays influence the perception of authenticity in a smile, with smiles with a longer onset- and offset-duration being considered as more genuine. In the same line, temporal aspects of the contraction of facial muscles in the production of "eye-brow-flashes" have an effect on the decoding process by an observer (Grammer, Schiefenhövel, Schleidt, Lorenz, & Eibl-Eibesfeldt, 1988). In this line, Grammer, Filova & Fieder (1997) aptly state that various kinematic elements contribute to the impression elicited by a nonverbal cue „By raising an arm fast or slow, with fist clenched or not, the movement staying at the maximum flexion for a certain time and going back fast or slowly" (p. 99) a variety of meanings may be conveyed.

Interestingly, such spatiotemporal properties, like duration, acceleration, rhythm and succession of actions, can not only describe one individual's movements, but also the social dynamics of an interacting dyad (Georgescu et al., 2013; Santos, David, Bente, & Vogeley, 2008). Indeed, research was able to show that flexible, online kinematic adjustments occur between partners during a dyadic interaction (for a review see Becchio, Sartori, & Castiello, 2010).

To conclude, it becomes evident that subtle movement dynamics influence how nonverbal behaviors are perceived and interpreted by an observer. Some research indicates that the subtle dynamics of movements may even have a stronger impact on the observer's impressions than so-called semantic aspects (i.e. a predefined ascribed meaning; Grammer, Honda, Juette, & Schmitt, 1999). It is therefore imperative that the nonverbal behavior research further acknowledges the importance of such dynamic properties of movement and focuses on them in order to be able to better characterize their influence on cognitive processes of information decoding and impression formation. In this regard, Burgoon and colleagues (1989) suggest that "we need to understand nonverbal communication as an ongoing, dynamic process rather than just a static snapshot of cues or final outcomes at one moment of time" (p. 23).

1.2 Methodological Approaches to the Study of Dynamic Nonverbal Cues

Research investigating effects of nonverbal behavior is confronted with several basic methodological problems. One of these problems concerns the fact that nonverbal behaviors are both encoded and decoded automatically and outside awareness (Choi et al., 2005). Thus, considering that throughout development human observers learn to extract information from nonverbal cues implicitly, it is important that we include both explicit and implicit measures in our investigation of the perception of nonverbal behaviors. Therefore, in addition to evaluative and person judgment tasks, which target explicit attitudes towards the stimulus material, functional magnetic resonance imaging (fMRI) opens up another level of analysis. This is particularly useful, since the automatic cognitive response to visual stimuli is not consciously accessible, hence, the neural correlates may even be more informative of an underlying cognitive process than its behavioral correlates. FMRI is a method for measuring brain activity within a strong static magnet field combined with radio wave pulses and gradients (Heeger & Ress, 2002; Horwitz, Friston, & Taylor, 2000). It is an indirect measure because it does not measure neural activity per se, but it only measures the secondary physiological changes, which are brought upon by neural activity. This has been termed the so-called blood oxygenation level-dependent (BOLD) effect. Cognitive processing is associated with an increase in neuronal firing rates and this increased neural activity leads to increased metabolic requirements for the neurons. Consequently, a series of physiological changes in the local network of blood vessels takes place, including cerebral blood volume and blood flow. 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; Horwitz et al., 2000). 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). FMRI has several advantages over other brain imaging techniques. First, it noninvasively records brain signals without the risks associated with radiation exposure inherent in other scanning methods, such as X-ray Computed Tomography and Positron Emission Tomography. Second, it has high spatial resolution (Heeger & Ress, 2002; Horwitz et al., 2000). Third, its recording is not limited to the cortical surface as is the case for Electroencephalography (EEG) and Magnetoencephalography (MEG) (Horwitz et al., 2000).

Another important tool for nonverbal research are virtual characters. They provide an experimental apparatus that has i) the potential to be controlled more precisely than any human actor, and ii) the advantage of physical presence and ecological validity (Vogeley & Bente, 2010). Their use as stimulus material in research studies enables more flexibility in experimental designs, by allowing i) the dissociation of movement information from appearance information and ii) the fine-grained and highly controlled manipulation of parameters of interest (ibid.). The utility and validity of digital simulation techniques in nonverbal behavior research has been amply demonstrated in previous studies, showing that character animations of nonverbal behavior lead to realistic social impressions and highly correlate with judgments based on live-action video recordings (Bente G., Krämer N.C., Petersen A., & De Ruiter J.P., 2001; G Bente, Petersen, Krämer, & de Ruiter, 2001).

1.3 The Neural Mechanisms of Processing Human Actions

An essential line of research in social cognitive science has been concerned with the investigation of the ability to understand other persons. The ability to perceive and understand others' socially meaningful movements relies on the integration of information into relevant motion cues, leading to ascriptions of mental states to others (Santos et al., 2010). The neural mechanisms subserving these processes are described below.

The neural mechanisms that enable observers to identify "what" other people are doing have been robustly associated with the so-called action observation network (AON, Julie Grèzes et al., 2001; Marsh et al., 2010; Saygin, 2007; see Fig. 1). This network includes the bilateral posterior superior temporal sulcus (pSTS), the inferior parietal lobe (IPL) and a premotor node, which encompasses the inferior frontal gyrus (IFG, pars opercularis), the ventral and dorsal premotor cortices (PMv, PMd) and the supplementary motor area (SMA). For example, research has shown that the perception of biological motion (i.e. seeing point-light displays (PLDs) of a human performing articulated movements) is associated with increased activation in the pSTS and the premotor cortex (PM) (Bonda, Petrides, Ostry, & Evans, 1996; Saygin, 2007). The AON has also been engaged by observing people perform various instrumental, transitive actions (i.e. manipulating an object), but also by intransitive actions, be they communicative (e.g. Lotze et al., 2006; Schippers, Gazzola, Goebel, & Keysers, 2009), expressive (e.g. Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; J Grèzes, Wicker, Berthoz, & de Gelder, 2009), or symbolic actions (e.g. Désy & Théoret, 2007; Molnar-Szakacs, Wu, Robles, & Iacoboni, 2007; Montgomery, Isenberg, & Haxby, 2007; Villarreal et al., 2008) and even during nonverbal communicative interactions (Centelles, Assaiante, Nazarian, Anton, & Schmitz, 2011). It has been proposed that it performs an automatic kinematic analysis of movements with respect to goal-intentionality (Santos et al., 2010).

However, the question of understanding "why" people are performing actions has been associated with a more inferential processing, often termed as "mentalizing" (Frith & Frith, 2003). This refers to the ability to attribute mental states (i.e. thoughts, emotions, beliefs and intentions) to other people and is also known as a Theory of Mind (ToM, Premack &

Woodruff, 1978). Thus, mentalizing refers to an explicit reasoning about other people's minds. Studies investigating mentalizing processes have found a set of brain regions that seems to be dedicated to such social cognition, namely the so-called social neural network (SNN; Adolphs, 2009; Frith, 2007; see Fig. 1). The SNN is thought to include regions along the cortical midline and in the temporal lobes, namely the medial prefrontal cortex (mPFC), the posterior cingulate cortex (PCC), the temporoparietal junction (TPJ) and adjacent pSTS as well as the insular cortex and the temporal poles (TP) (ibid.). For example, studies asking participants to evaluate nonverbal behavior e.g. (Kuzmanovic et al., 2012), to infer the mental states from the eye region (Baron-Cohen et al., 1999), or to think about the motivations behind actions (Brass, Schmitt, Spengler, & Gergely, 2007) have been found to elicit activation in areas of the SNN.

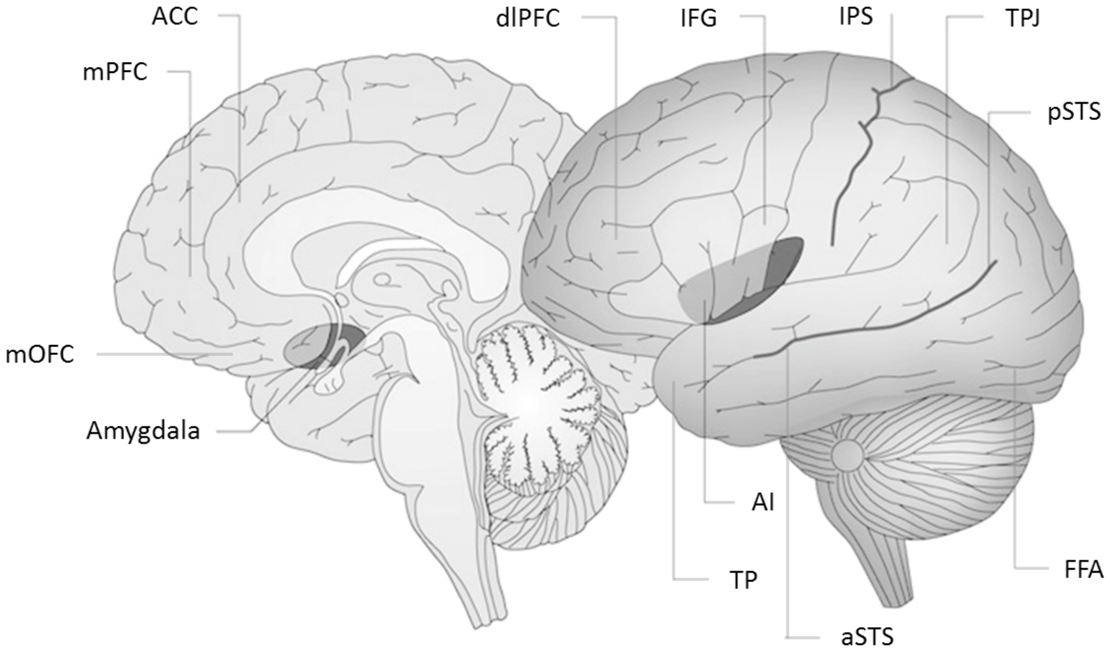

Figure 1. Action Observation Network (AON) and Social Neural Network (SNN). Depicted are the key regions involved in social cognition in a medial and lateral view of the brain. See text for details and abbreviations (adapted from Blakemore, 2008).

Both networks, the AON and the SNN have been proposed to be involved in understanding the intentions behind others actions and may have distinct but complementary functions (De Lange, Spronk, Willems, Toni, & Bekkering, 2008; Keysers & Gazzola, 2007; Uddin, Iacoboni, Lange, & Keenan, 2007; Zaki, Hennigan, Weber, & Ochsner, 2010). More specifically, it has been proposed that the AON is required for both low- and high-level identification of actions and the SNN is required for high-level conscious mental inference and evaluation of social stimuli (Brass et al., 2007; de Lange et al., 2008; Keysers & Gazzola, 2007; Santos et al., 2010; Spunt, Falk, & Lieberman, 2010; Spunt, Satpute, & Lieberman, 2011; Thioux, Gazzola, & Keysers, 2008; Uddin et al., 2007; Van Overwalle & Baetens, 2009). In other words, the AON encodes the observable, perceptual-motor properties of others' actions and the SNN interprets those properties in terms of unobservable mental states and traits. Despite the fact that the AON and SNN are rarely concurrently active (for a review, see Van Overwalle & Baetens, 2009), it seems that under specific conditions both systems might be involved in the processing of whole-body nonverbal behavior during social interactions (e.g. Centelles et al., 2011). Thus, the exact relationship between SNN and AON is complex and still to be explored.

1.4 High-Functioning Autism and the Processing of Nonverbal Cues

High-functioning autism (HFA) is a pervasive neurodevelopmental disorder of the autism spectrum that is characterized by sociocommunicative impairments on the one hand but intact non-social cognitive capacities on the other (Klin, 2006). More specifically, one of the core deficits of individuals with HFA concerns the interpretation of nonverbal behaviors. For instance, individuals with autism show an atypical processing and decoding of nonverbal cues such as facial expressions and gaze behavior (Senju & Johnson, 2009a; Uljarevic & Hamilton, 2013). However, deficits in processing dynamic aspects of nonverbal behavior in single-agent and dyadic contexts have also been observed: Individuals with Autism Spectrum Disorder (ASD) have not only been shown to have both a compromised perception of biological motion (for a review, see Kaiser & Pelphrey, 2012) but also a deficit in the detection of social contingencies (Castelli, Frith, Happé, & Frith, 2002; Gergely, 2001; Klin, 2000). In the same line, a recent study by Centelles, Assaiante, Etchegoyhen, Bouvard and Schmitz (2013) has found that autistic children were less accurate at deciding whether two point-light characters were communicating or not based on their movement patterns alone. Furthermore, some person perception studies have come to the conclusion that the degree to which nonverbal information contributes to complex subjective social decisions is significantly lower in individuals with HFA than in typically developing individuals (Kuzmanovic, Schilbach, Lehnhardt, Bente, & Vogeley, 2011; Schwartz, Bente, Gawronski, Schilbach, & Vogeley, 2010).

To conclude, investigating the neural processing of nonverbal behavior in HFA promotes a better understanding of this disorder and additionally enables a better specification of the mechanisms underlying social cognition in healthy individuals.

1.5 Aim of the Current Thesis

With the present studies we hoped to address several open questions in the field of nonverbal behavior research. One question concerned the validity of using virtual characters as a tool for investigating dynamic aspects of nonverbal behavior in neuroimaging studies (Studies 1-4). Another question concerned the contribution of different dynamic movement characteristics to the processing of nonverbal behavior. More specifically, we focused on the duration of social gaze cues (**study 1** and **study 2**), the kinematics of biological motion (**study 3**) and the contingency of movement patterns in a dyadic context (**study 3** and **study 4**). Further, we sought to contribute to the ongoing debate on how the two neural networks AON and SNN are involved in ascribing meaning to movements (**study 3**). Finally, the question of perturbations of nonverbal processing in HFA was addressed (**study 2** and **study 4**). Thus, in four different experiments (two published, one accepted, one under revision), we used methodologies such as fMRI, virtual characters and experimental psychological paradigms in order to address the aforementioned questions.

2 Studies 1 and 2: The Dynamics of Social Gaze

2.1 Theoretical Background

2.1.1 The Role of Gaze Behavior in Social Cognition

The eye region provides essential information related to a person's identity, emotional state and focus of attention (Kleinke, 1986). Interestingly, eyes have even been proverbially referred to as a "window to the soul". Indeed, the perceived gaze behavior of another person allows inferences about their underlying mental states (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001; Simon Baron-Cohen, Wheelwright, & Jolliffe, 1997; Eskritt & Lee, 2007). Consequently, being able to accurately attribute mental states of our social others based on their social gaze cues allows for the coordination of attention and activities between interaction partners (Argyle & Cook, 1976; Kleinke, 1986).

In particular, the direction of perceived gaze is important. As an indicator of another's focus of attention (Mason, Tatkow, & Macrae, 2005), perceived direct gaze may express social interest and the intention to communicate (Cary, 1978; Kleinke, 1986). A sensitivity to direct gaze is seen from a very early age, with newborns spending more time looking at faces with direct compared to averted gaze (e.g. Farroni, Csibra, Simion, & Johnson, 2002). Research has repeatedly shown that direct gaze is detected faster and more accurately than averted gaze (Conty, Tijus, Hugueville, Coelho, & George, 2006; Senju, Kikuchi, Hasegawa, Tojo, & Osanai, 2008; Senju, Tojo, Yaguchi, & Hasegawa, 2005; Senju, Yaguchi, Tojo, & Hasegawa, 2003; Wallace, Coleman, Pascalis, & Bailey, 2006). Moreover, direct gaze, as compared to averted gaze, has been shown to modulate various aspects of cognitive and attentional processing, a phenomenon termed as the so-called "eye-contact effect" (Senju & Johnson, 2009b). In this line, direct gaze facilitates performance in gender discrimination tasks (Macrae, Hood, Milne, Rowe, & Mason, 2002), facial identity recognition tasks (Hood, Macrae, Cole-Davies, & Dias, 2003; Smith, Hood, & Hector, 2006) and person memory tasks (Mason, Hood, & Macrae, 2004) and has an enhancing effect on likeability and attractiveness ratings of others (Mason et al., 2005).

However, it is important to note that, not only the direction of perceived gaze is informative during person perception, but also more dynamic aspects of gaze behavior (Foa, Foa, & Schwarz, 1981). For example, the same direct gaze cue may have multiple meanings depending on more subtle aspects of the behavior: Standing by the side of a road and making eye contact with drivers either with the intention of demanding a lift (i.e. hitch-hiking; Ellsworth, Merrill, & Henson, 1972) or with no particular intention at all (Snyder et al., 1974) increased the likelihood of actually receiving a lift in the first study but not in the second one. One such dynamic aspect of gaze behavior is its duration. For example, being looked at longer than a short glance results in more compliance with a request (Guéguen & Jacob, 2002). Moreover, humans learn to use the relative gaze duration towards different objects in the environment to infer other people's preferences (Einav & Hood, 2006; Montgomery, Bach, & Moran, 1998). In terms of person perception, when a target person is displaying prolonged direct gaze toward an observer, the former are rated as more likeable (Argyle, Lefebvre & Cook, 1974), potent (Brooks, Church, & Fraser, 1986) and as having more self-esteem (Droney & Brooks, 1993). In the context of social interactions, sustained mutual eye contact can moderate interpersonal distance (Argyle & Dean, 1965). In this line, increasing perceived duration of direct gaze can enhance the degree of intimacy between interaction partners and, depending on the context, evoke the impression of either affiliation or threat (Argyle, Lefebvre & Cook, 1974). In the same line, Ellsworth and colleagues (1972), have suggested that "the stare, in effect, is a demand for a response, and in a situation where there is no appropriate response, tension will be evoked, and the subject will be motivated to escape the situation" (p311).

Taken together, social gaze cues provide unique access to investigate critical mechanisms of social cognition. While the perception of gaze direction has been investigated more extensively in the past, dynamic aspects of gaze behavior have not been comprehensively looked at, despite the fact that they are known to modulate the communicative content transmitted by the eyes (Argyle & Cook, 1976; Kleinke, 1986).

2.1.2 Neural Correlates of Social Gaze Processing

Electrophysiological evidence has indicated differential neural activity for direct versus averted gaze (Conty, N'Diaye, Tijus, & George, 2007; Gale, Spratt, Chapman, & Smallbone, 1975; Hietanen, Leppänen, Peltola, Linna-Aho, & Ruuhiala, 2008; Senju et al., 2005). For example, recent event-related potential evidence showed that the dissociation between direct and averted gaze processing occurs as soon as 160 ms, and source reconstruction showed that it involved regions of the SNN (Conty et al., 2007). FMRI studies have further explored the cortical networks involved in processing gaze direction (for reviews, see Grosbras, Laird, & Paus, 2005; Itier & Batty, 2009; Nummenmaa & Calder, 2009; Senju & Johnson, 2009b). In a recent review, Senju and Johnson (2009b) mention a total of six regions which have been reported to show differential activity between direct and averted gaze, namely the fusiform gyrus (FG), the posterior superior temporal sulcus (pSTS), the dorsomedial prefrontal cortex (dmPFC), the orbitofrontal cortex (OFC) and the amygdala. These regions are known to be part of the SNN, which is required for conscious mental inference and evaluation of social stimuli (Van Overwalle & Baetens, 2009). Interestingly, not all social gaze studies have found activations in all of these regions of the SNN since the neural response to gaze direction interacts with task demands and context, to influence precisely which ones are engaged (Senju & Johnson, 2009b).

2.1.3 Social Gaze Processing in Individuals with HFA

In autism spectrum disorders, atypical processing of eye stimuli have been repeatedly observed (Senju & Johnson, 2009a). For example, autistic persons are impaired in reading others' mental states from the eye region (Baron-Cohen et al., 2001). A series of behavioral studies have demonstrated that direct gaze does not elicit the so-called "eye contact effect" in individuals with autism. This means that perceived eye contact is neither preferred by nor does it offer any perceptual advantage or modulate cognition and attention in autistic persons (for a review, see Senju & Johnson, 2009a). For example, individuals with autism spectrum disorders have been found to be equally efficient in detecting direct as well as averted gaze and did not show the facilitative effect of eye contact characteristic for typically developing participants (Senju et al., 2003). Furthermore, an absence of a preferential reaction to gaze in contrast to non-biological cues has been found repeatedly (e.g. Ristic et al., 2005; Senju, Tojo, Dairoku, & Hasegawa, 2004). For instance, Vlamings, Stauder, Van Son and Mottron (2005) showed that arrows and eye stimuli triggered attention in the same way in autistic persons whereas control participants showed faster reaction times for the eyes.

Only two fMRI studies so far have investigated the neural processing of direct compared to averted gaze in individuals with HFA relative to a control group in a realistic situation (Hagen, Stoyanova, Rowe, Baron-Cohen, & Calder, 2013; Pitskel et al., 2011). Both studies used computer-generated characters to implement two gaze direction conditions (toward the viewer and away from them). Despite the differing context and task demands, both studies reached similar conclusions: They found that regions of the SNN were engaged by direct compared to averted gaze in control but not in HFA participants and suggested that this was due to the fact that direct gaze was a less salient stimulus for autistic participants. Interestingly, it has been suggested that gaze processing deficits in HFA result from an impairment to extract relevant information from the eye region necessary for social communication (Pelphrey, Morris, & McCarthy, 2005). However, in order to answer this question, experimental paradigms need to allow for the dissociation of social perception of gaze cues on the one hand and social processing thereof on the other. It is thus important to take a closer look, not only at gaze direction but also at specific subtle aspects of gaze behavior, like duration, as well as their neural correlates to determine how exactly individuals with ASD perceive and process gaze stimuli differently compared to neurotypical individuals. To our knowledge, this is the first investigation of the processing of both gaze direction and duration in adults typically developed adults and individuals with HFA, which allowed us to investigate detection and evaluation processes with the same stimulus material.

2.2 Experimental Design and Hypotheses

The aim of **study 1** and **study 2** was to investigate the influence of the two factors gaze direction and gaze duration on the judgment of likeability of virtual human faces in HFA participants and typically developed individuals.

The paradigm used by both studies had a two by three factorial design with the two factors (a) gaze direction, varied on two levels (direct or averted) and (b) gaze duration varied on three levels (1, 2.5 and 4 seconds) (see Fig. 2). The stimulus material consisted of 20 computer-generated faces (10 male and 10 female) created using the commercially available 3D animation software Poser 6.0 (Curious Labs Inc. Santa Cruz, USA). Each trial began with the display of a face, the gaze of which was initially averted. After a short blink (150 ms), the character directed its gaze toward the participant and after a variable period of time (depending on the condition of interest, either 1, 2.5 or 4 seconds), the virtual character looked again away by shifting its gaze back to the initial position. The task required participants to watch each animation and evaluate the likeability of the animated faces on a four-point likeability scale (see Fig. 2). 22 right-handed participants (12 male; mean age: 27.2 ± 3.9 years) took part in **study 1**. A group of 13 HFA individuals (9 male; mean age: 31.23 ± 4.87 years) participated in **study 2.** They were diagnosed and recruited in the autism outpatient clinic at the Department of Psychiatry of the University Hospital of Cologne in Germany. Furthermore, 13 matched control participants (9 male; mean age: 30.23 ± 3 years; some were from **study 1**) volunteered to take part in **study 2**.

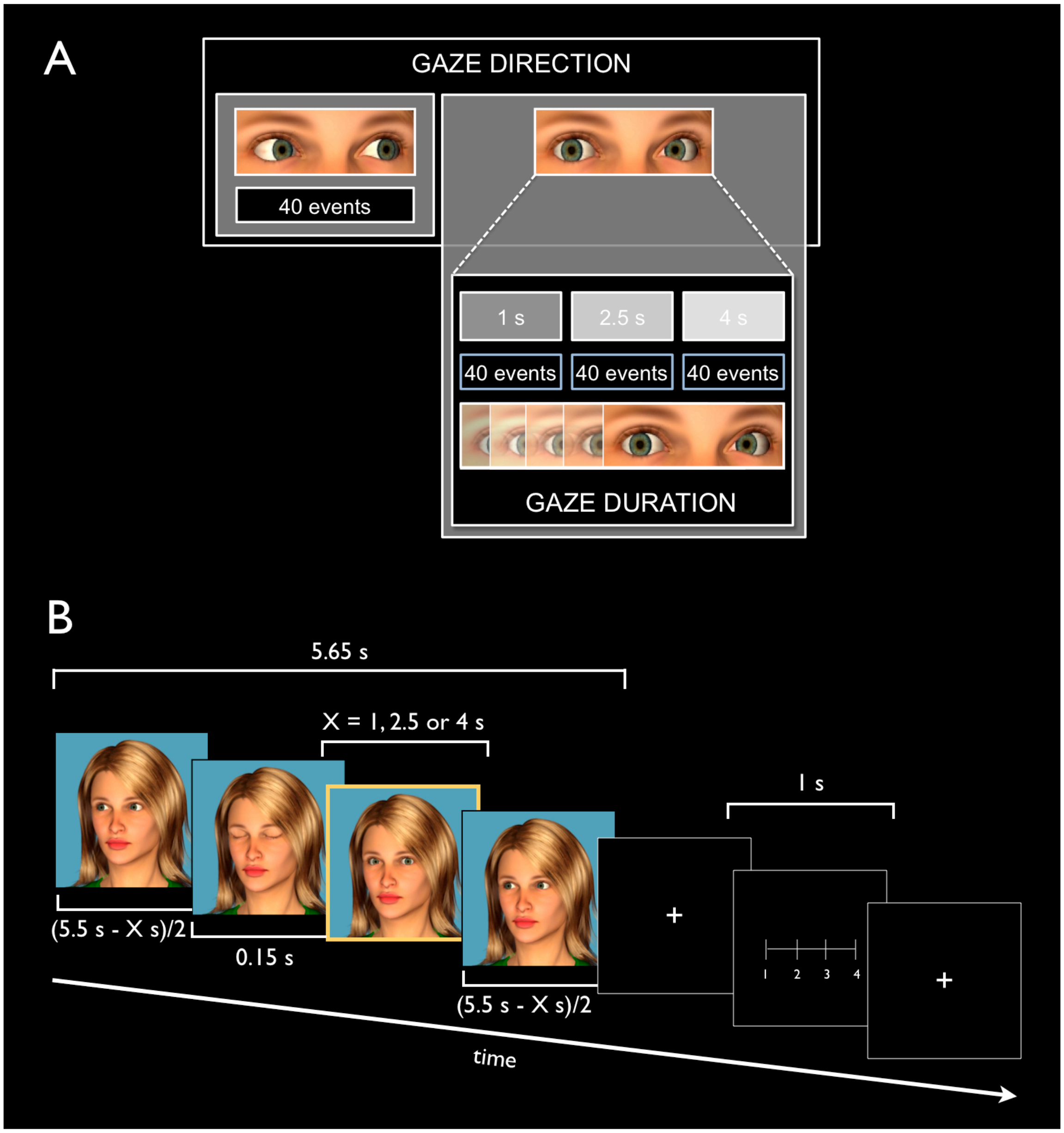

Figure 2. A. Experimental design. B. An example of a virtual face stimulus and a sample direct gaze trial. The participants' task was to observe and rate the perceived likeability of each face on a 4-point scale.

We hypothesized that, in typically developed individuals, direct compared to averted gaze would activate the pSTS, a region that has been robustly linked to the perception of gaze behavior (Bristow, Rees, & Frith, 2007; Calder et al., 2002; Ethofer, Gschwind, & Vuilleumier, 2011; Hagen et al., 2013; Pelphrey, Viola, & McCarthy, 2004; Pitskel et al., 2011). Further, we assumed that increasing gaze duration would engage the mPFC, a region associated with the evaluation of social stimuli (Amodio & Frith, 2006; Zysset, Huber, Ferstl, & von Cramon, 2002). We further assumed that these effects would be weaker or absent in participants with HFA, given the fact that direct gaze may hold less salience for them (Senju & Johnson, 2009a).

2.3 Findings and Conclusions

Behavioral data were tested by a two-way repeated measures analysis of variance (ANOVA) using SPSS (PASW Statistics 18). Results revealed that HFA participants showed no significant difference in likeability ratings depending on gaze duration, while the control group rated the virtual characters as more likeable with increasing gaze duration (see Fig 2). The behavioral analysis revealed no main effect of gaze duration (F(2, 48) = 1.1, p = .34) or group (F(1, 24) = 2.92, p = .1), possibly because of the low sample size (see Fig. 3).

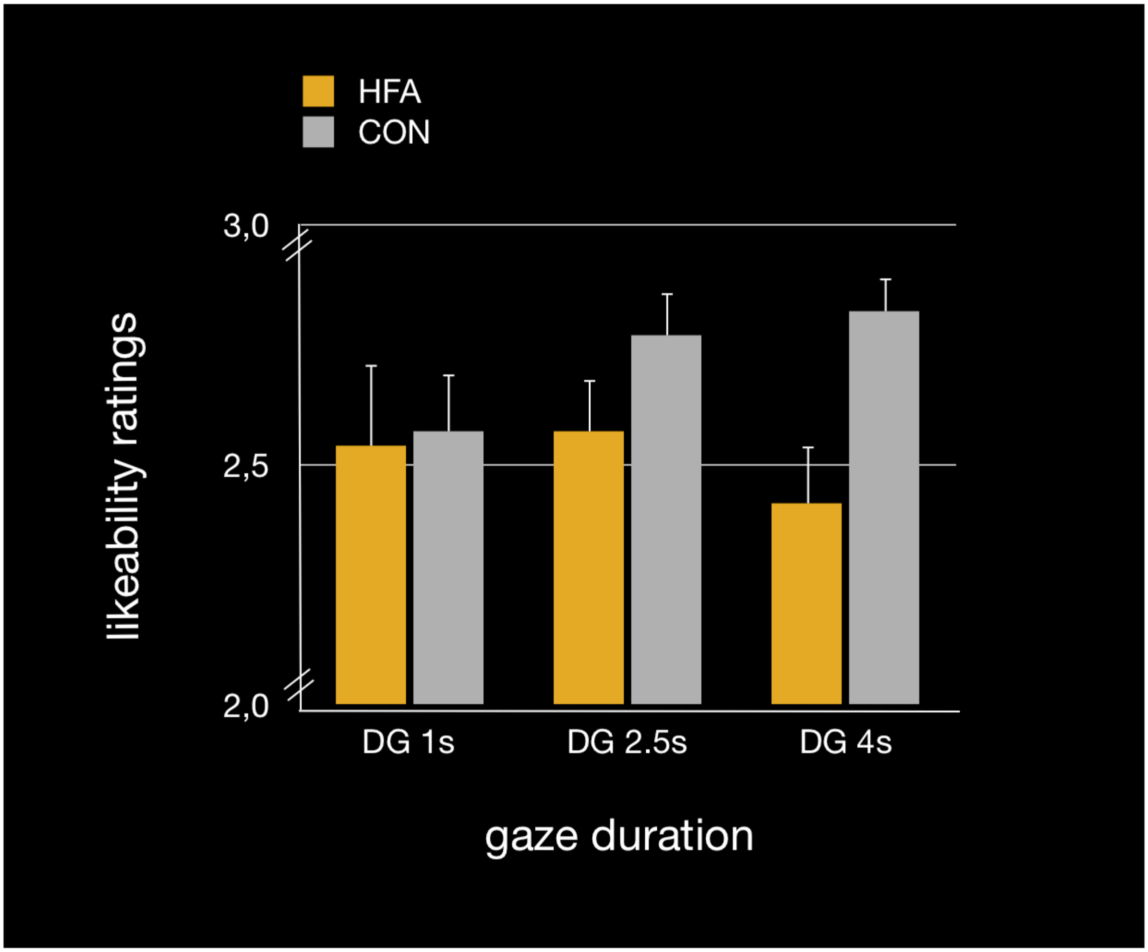

Figure 3. The plot illustrates the effects of gaze duration on likeability ratings. The scales on the y-axis indicate the mean of stimuli ratings. A score of 1 refers to rating a face as “dislikable” and one of 4 as “likeable”. Error bars show 1 standard error of the mean. HFA = High-functioning autism; CON = Control group

In terms of neural activations, both **study 1** and **study 2** suggest that there are two complementary cognitive processes related to the two factors gaze direction and duration for typically developing adults. Furthermore, these processes seem to recruit distinct neural areas within the SNN. On the one hand, the recruitment of the pSTS, the insula, the PCun and the TPJ for processing direct compared to averted gaze indicates salience detection. On the other hand, a parametric analysis of the processing of increasing gaze duration revealed the involvement of regions of the mPFC (the dACC and the mOFC). These regions are typically associated with outcome monitoring, hence indicating higher-order social cognitive processes related to the evaluation of the ongoing communicational input conveyed by prolonged eye contact. However, in the HFA group, solely the pSTS was engaged by direct compared to averted gaze, while several regions of the SNN, namely the PCun, the TPJ and the FG were activated by the opposite contrast. This result supports previous research findings demonstrating atypical neural processing of gaze direction in autistic individuals relative to a control group (Grice et al., 2005; Hagen et al., 2013; Pitskel et al., 2011, 2011; Senju et al., 2005). Moreover, in the HFA group, while processing increasing gaze duration did not elicit any differential activations, decreasing gaze duration was correlated with neural activity in the PCun (see Fig. 4). The analysis of the group x condition interaction evaluating brain regions more responsive to direct than to averted gaze in the typical compared to the HFA group, revealed activations in the mOFC, the right Cun and PCun, left MTG, extending to the aSTS and bilaterally the TPJ (localized in the posterior terminal of the ascending branch of the STS; see Fig. 3).

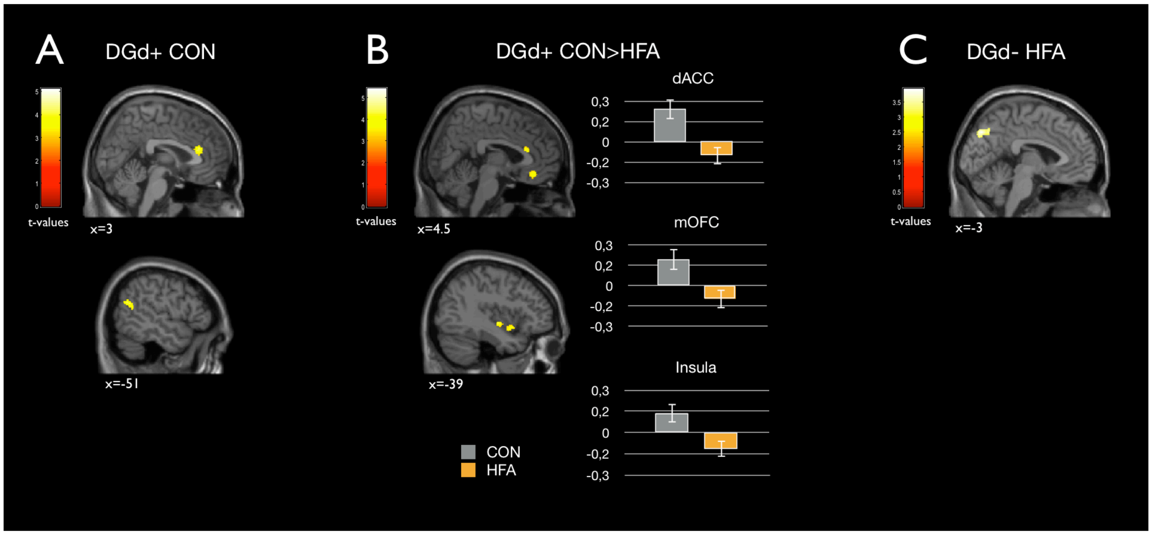

Figure 4 Neural Results of Study 2: Gaze Duration. A. Neural activation associated with increasing gaze duration for the control group. B. Direct group comparison between the control and HFA group for the neural processing of increasing gaze duration. Plots illustrate corresponding contrast estimates obtained for the four stimulus categories for three different local maxima: left dACC (-9, 33, 15), right mOFC (11, 38, -17) and left insula (-38, -9, -6). Error bars represent confidence intervals. C. Neural activation associated with decreasing gaze duration for the HFA group. The principally activated voxels are overlaid on the mean structural anatomic image of the 26 participants: $p < .001$, cluster-level corrected; DGd+ = increasing direct gaze duration; DGd- = decreasing direct gaze duration; CON = control group; HFA = high-functioning autism group; dACC = dorsal anterior cingulated cortex; mOFC = medial orbitofrontal cortex.

While direct gaze and increasing direct gaze duration may signal social salience and a communicative intent to typically developing individuals, gaze duration does not hold the same relevance for individuals with HFA. However, the present results also demonstrate, that in participants with HFA, gaze processing deficits are not based on gaze direction discrimination per se. Thus, it is not a deficit in perception of social stimuli but in the processing thereof. Rather, they seem to result from atypically ascribing salience and from being impaired in using subtle aspects of gaze, such as the duration of direct gaze, to understand others.

3 Study 3: Neural Correlates of the Perception of Nonverbal Behavior in Dyadic Interactions

3.1 Theoretical Background

3.1.1 The Importance of Whole-Body Movements in Social Cognition

As previously stated in the introduction (chapter 1.1), nonverbal meaningful information is not only conveyed by specific gestures, facial expressions or body postures, but also by full-body movements (Santos et al., 2008). Interestingly, it seems that even in earliest stages of development, humans are sensitive to the kinematic properties of biological motion. Indeed, a great number of studies have suggested that people are able to implicitly extract information about observed activities, identities, emotions, and context from the kinematic information inherent in a movement (for a review, see Blake & Shiffrar, 2007; Knoblich, 2006). Moreover, this is not only the case for individual actions but also for actions performed in an interacting context: Dyadic interactions such as dancing, sparring or shaking hands can be accurately identified when presented as reduced-cue stimuli (e.g. Centelles et al., 2011; Dittrich, 1993).

3.1.2 Generating Mental State Content Based on Movement Characteristics: The Case of Movement Fluency and Contingency Information

Two important kinematic properties of human movement are 1) movement fluency and 2) movement contingency (Blakemore et al., 2003; Georgescu et al., 2013). While the first can be described as a characteristic of the movements of an individual agent, the latter describes the spatiotemporal dynamics between agents and is a characteristic of the dyad.

Human movements are characterized by a smooth velocity, following a bell-shaped acceleration profile, the so-called minimum-jerk velocity (Hogan, 1984). The velocity is smooth, because, mathematically, the derivative of acceleration (i.e. "jerk") is minimized over the movement trajectory (Abend, Bizzi, & Morasso, 1982). Another way of describing this kinematic characteristic of biological motion is by using the two-thirds power law of motion. This law suggests that biological movements slow down at curved relative to straight parts of the trajectory (Lacquaniti, Terzuolo, & Viviani, 1983). Indeed, (Morewedge, Preston, & Wegner, 2007) have found that human and nonhuman targets (be they animals, robots and animations) are more likely to be considered to possess mental states when they move "at speeds similar to the speed of natural human movement" (p.1). In the same line, research has found that movements that follow such a smooth velocity profile are more likely to be perceived as intentional and animate (Pyles, Garcia, Hoffman, & Grossman, 2007). To conclude, we will continue to refer to this characteristic of biological motion, which describes a smooth velocity profile, as movement fluency.

Apart from the physical properties of biological motion itself, the complex dynamics of movement patterns also facilitate the perception of meaning in a visual stimulus. Anecdotal evidence, as well as scientific research has found that human observers tend to interpret an interaction between moving non-biological objects as a social encounter when their movement patterns are contingent (Castelli, Happé, Frith, & Frith, 2000; Gobbini, Koralek, Bryan, Montgomery, & Haxby, 2007; Santos et al., 2010, 2008; J. Schultz, Friston, O'Doherty, Wolpert, & Frith, 2005; Schultz, Imamizu, Kawato, & Frith, 2004). In the context of social interaction research, the term "social contingency" has been used to describe an above chance probabilistic mutual relationship between the actions of two interactants (Moran et al., 1992). Humans are able to extract information about social contingencies to identify categories of interaction such as playing, fighting, chasing etc (Berry, Misovich, Kean, & Baron, 1992; Bloom & Veres, 1999; Blythe, Miller, & Todd, 1996; Rimé, Boulanger, Laubin, Richir, & Stroobants, 1985; Scholl & Tremoulet, 2000). The available cues that might enable humans to access such information include timing and spacing contingencies (Gergely and Watson 1999). Thus, henceforth we refer to contingency as the "noncoincidental bidirectional coordination of movement patterns both in the temporal and the spatial domain between two interacting agents, which result in meaningful patterns of mutual social coordination" (Georgescu et al., 2013).

3.1.3 Neural Correlates of Generating Mental State Content Based on Movement Stimuli

3.1.3.1 Neural Correlates of Processing Biological Movements

The involvement of the AON in the perception of biological motion has been previously attested (e.g. Saygin, Wilson, Hagler, Bates, & Sereno, 2004; Saygin, 2007). In fact, it has been suggested that the AON might be tuned specifically to biological motion and that it would respond to a lesser extent to nonbiological or robotic movements (Casile et al., 2010; Dayan et al., 2007; Kilner, Paulignan, & Blakemore, 2003; Press, 2011). Two fMRI studies indicated that, both when stimuli are of point (Dayan et al., 2007; BA6 and BA44) and human form (Casile et al., 2010; BA6), observing movements obeying the two-thirds power law activates premotor structures to a greater extent than observing movements with the inverted kinematic profile. Press and colleagues (2011) presented the participants of an MEG study with human form or point form arm movements, which moved with human or constant velocity profiles. Only when observing movements with biological velocity (irrespective of form), sensorimotor activation changed across time in a manner that would be expected if executing the actions. In order to investigate the influence of kinematics on social perception, research is increasingly relying on robotic stimuli to operationalize nonbiological movement. Tai, Scherfler, Brooks, Sawamoto, & Castiello (2004), for example, found a significant neural response in the left premotor cortex, a key node of the

AON, for subjects observing manual grasping actions by a human but not by a robot model. Nevertheless, findings in this research area are still inconclusive, since two fMRI studies found that the AON was strongly activated by the sight of both human and robotic actions, with no significant differences between the two (Gazzola, Rizzolatti, Wicker, & Keysers, 2007; Oberman, McCleery, Ramachandran, & Pineda, 2007). The inconsistency in previous findings may be due to the fact that often motion kinematics are confounded with appearance information, and it is not clear neither which factors contribute to the findings, nor to what extent they do so. In fact, it is most likely that an interaction between kinematics, agent form and task demands might modulate social perception (Cross et al., 2011; Saygin, Chaminade, Ishiguro, Driver, & Frith, 2011). Thus, it is important to study how movement fluency modulates AON activity, when appearance information is not confounded with kinematic information.

3.1.3.2 Neural Correlates of Processing Contingent Movement Patterns

Observing contingent movement patterns between objects can elicit increased neural activation in the SNN (Castelli et al., 2000; Castelli et al., 2002; Martin & Weisberg, 2003; Ohnishi et al., 2004; Tavares, Lawrence, & Barnard, 2008). The pSTS, for example, is activated not just by the perception of human biological motion (Allison, Puce, & McCarthy, 2000; Bonda et al., 1996; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004), but also by movements of nonbiological agents, when exhibiting intentionality as reflected by interactive dynamics (Castelli et al., 2000; Gobbini et al., 2011; Santos et al., 2010; Schultz et al., 2005, 2004). Further, Castelli and colleagues (2000) performed a PET study and used animations of moving geometric figures, similar to those developed by Heider and Simmel (1944). They found increased activations in ventral mPFC and temporal regions (FG and TP), when comparing contingent with random motion animations. Such findings support the so-called “intentionality hypothesis”, which claims that the impression of an animate and mindful agent is not based on motion information alone but includes inferences about the causes of these motions (Gelman, Durgin, & Kaufman, 1995; Santos et al., 2008).

3.1.3.3 Neural Correlates of Processing Dyadic Nonverbal Social Interactions

Despite the fact that social interactions are an abundant stimulus in our environment, surprisingly little research has studied how it is perceived and processed on a neural level.

Due to the methodological constraints mentioned in the introduction (chapter 1.2), some studies have used pictures of interacting individuals. For example, Walter and colleagues (2004) presented participants with cartoon stories of characters engaged in social interaction and asked them to chose a logical ending. They found that the mPFC is involved in understanding social intentions. Pierno, Becchio, Turella, Tubaldi and Castiello (2008) presented participants with pictures of triadic interactions between two individuals or with two actors performing individual object-related actions. The authors have found that the observation of social interactions evoked activity within the dmPFC, the PCun, IFG and angular gyrus (in the TPJ). Kujala, Carlson and Hari (2011) used still pictures of two individuals either facing toward or away from each other and a passive viewing task. Activations within the amygdala, pSTS and dmPFC were sensitive to the interactional position and distinguished humans facing toward from humans facing away. Finally, Canessa and colleagues (2012) used pictures of social interactions between two individuals (either cooperative or affective) and found that the right TPJ was involved in processing both types of interactions, suggesting that both situational contexts require the inference of action goals. Furthermore, while the AON was more involved in processing cooperative compared to affective interactions, the SNN was more engaged by the opposite contrast.

To this date, there have been only four neuroimaging studies using dynamic moving stimuli of humans engaged in nonverbal interactions. Hirai and Kakigi (2009) performed an MEG study to investigate the neural activity in response to the interaction information between two PLDs of motion-captured boxing agents who were either facing each other (interaction), or whose positions were swapped (no interaction). They have found that the interaction information can affect the neural activity in the bilateral occipitotemporal region, on average 300-400ms after the onset of a two-agent BM stimulus. Iacoboni and colleagues (2004) conducted an fMRI study that required participants to passively watch movie clips depicting everyday social interactions. The observation of the relational segment of the movie clip, during which two persons were interacting, compared to the observation of the segment of the movie clip depicting a single individual agent, yielded increased activity in two key areas of the SNN, the PCun and the dmPFC. Sinke, Sorger, Goebel and De Gelder (2010) investigated brain activity in subjects observing movie clips of two persons with blurred faces interact in two different contexts (teasing or threatening). They have found stronger amygdala activation for threatening than teasing interactions, regardless of whether the emotional context was attended to or not. In a recent study, Centelles and colleagues (2011) used fMRI and PLDs to investigate the perception of communicative interactions between two motion-captured agents. In the interaction condition, one actor performed a communicative action, which triggered a reaction from the other actor, and in the no interaction condition the two agents were moving independently side by side. Results showed that both the AON and the SNN were involved in the processing of the interaction condition versus the no interaction condition.

Yet, there are several shortcomings to these studies, which limit their interpretation. Hirai and Kakigi (2009) did use dynamic nonverbal interactions, however they were not communicative. Centelles and colleagues (2011) used communicative nonverbal interactions but they were short, ritualized behaviors, with a learned social response expectancy (e.g. directives like “come here” or “sit down”). While Sinke and colleagues (2010) and Iacoboni and colleagues (2004) did look at more complex communicative interactions, their research questions and contol conditions were either not robust enough or not focused on the relational component. To conclude, the main problem with the previous research is that it’s very hard to find i) an ecologically valid stimulus material that allows systematic manipulation of the parameters of interest; ii) a control condition where the relational aspect of an interaction is eliminated, without also eliminating the communicative aspect and iii) an appropriate control condition which ensures that low-level action features like the quantity of movement or the size or scale of the movements in space is comparable across conditions.

3.2 Experimental Design and Hypotheses

The major objective of the present fMRI study was to employ a novel design that would allow us to systematically manipulate both fluency and contingency information in nonverbal social interaction stimuli. This would help clarify the weight of these two factors in and the contribution of the two neural networks, AON and SNN, to the perception of nonverbal communicative interactions.

The paradigm used was adapted from a recently developed method to examine social interaction from a third-person perspective, (Bente et al., 2001; Bente, Senokozlieva, Pennig, Al-Issa, & Fischer, 2008). During fMRI 21 male participants (mean age: 26.86 ± 2.56 years) watched 10s long silent videos of communicative nonverbal interactions between two anonymous, standardized virtual agents. They were asked to rate on a four-point scale how natural they perceived each scene to be. We directly manipulated the movement fluency and contingency information present in the videos in a two-by-two factorial design. First, to manipulate the movement fluency, kinematics of the original dyads were changed in such a way that the movements would not comply with the two-thirds power law and would look rigid and jerky instead of smooth. Second, to manipulate the contingency information, the original dyads were changed in such a way that one of two interactants was substituted by the mirrored image of the other, resulting in the presentation of a single agent and its reflection about the midline. This effectively eliminated the contribution of one of the two agents from the interaction. Scrambled videos served as a baseline. Across conditions, we ensured that movement quantity was comparable (see Fig 5).

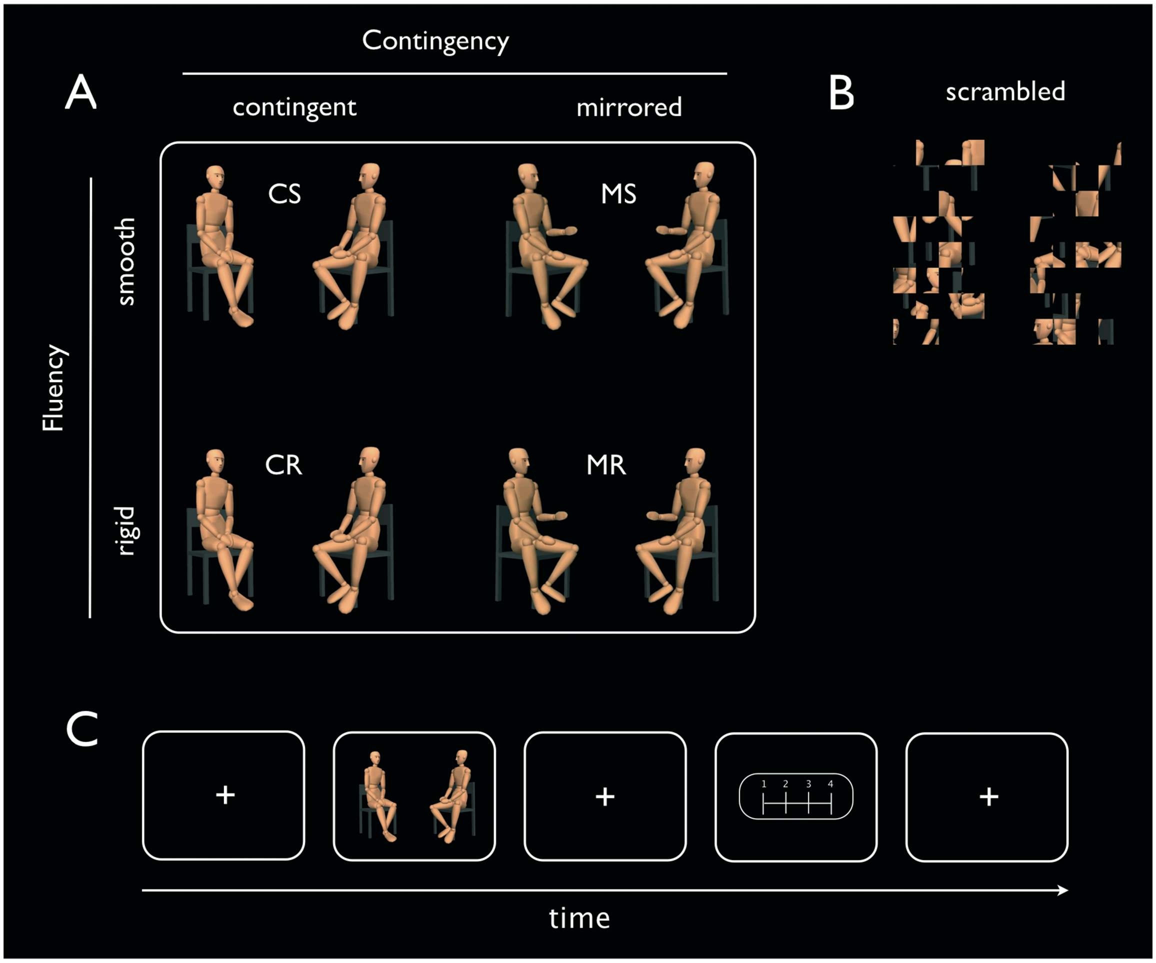

Figure 5. Design and Sample Stimuli of Study 3. A. Sample stimuli and the 2x2 factorial experimental design. CS = contingent + smooth; CR = contingent + rigid; MS = mirrored + smooth; MR = mirrored + rigid. B. Example of still caption of a scrambled video C. Example of an experimental trial: The participants' task was to observe each video and rate the perceived naturalness of each scene on a 4-point scale

We assumed that both factors would have an effect of the perceived naturalness of the scenes. In concordance with Centelles and colleagues (2011) we hypothesized that both the AON and the SNN would be involved in the processing of contingent information in the context of dyadic social interactions. With respect to the kinematics manipulation, we hypothesized that there would be no biological bias of the AON, because it would be the perceived communicative intentions which would drive the effect rather than movement fluency.

3.3 Findings and Conclusions

Behavioral data were tested by a two-way repeated measures analysis of variance (ANOVA) using SPSS (PASW Statistics 18) with contingency and fluency as within-subject independent variables. Results show that people are sensitive to contingency information (F(1, 20)=64.9, p<.0001) and to movement fluency (F(1,20)=57.4, p<.0001). Furthermore, there was a significant interaction effect between contingency and movement fluency (F(1,20)=31.2, p<.0001) indicating that contingent (compared to mirrored) movements increased naturalness ratings more in videos with smooth compared to rigid kinematics.

Neurally, we found that the perception of contingent compared to mirrored movements was associated with a significant increase of neural activity in the AON, involving bilaterally the IFG (extending bilaterally to the premotor cortex) the STG and pSTS, (extending to the extrastriate area), (see Fig. 6). This finding corroborates previous research and suggests that the stronger AON engagement for contingent patterns is likely related to the fact that processing the movements of a dyad requires more complex action representations than those of agents performing individual actions (Centelles et al., 2011). However, our design allows us to extend this claim by showing that, it is not just the communicative nature of perceived nonverbal movements but the inherent relational/reciprocal information, which defines the complexity of action representations. The lack of SNN activation for the processing of contingent information may seem surprising, however, the task of the present study rather triggered intuitive evaluation processes rather than inferential ones.

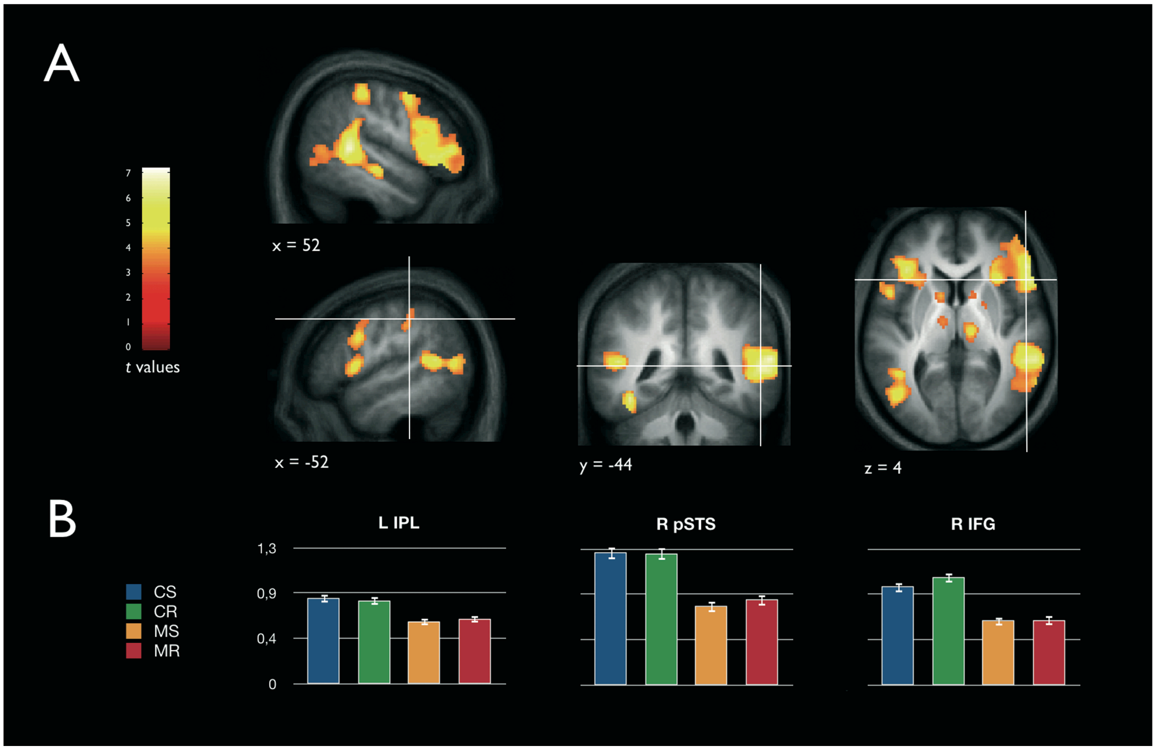

Figure 6. Neural Results of Study: Effects of Contingency. 3 A. Differential neural activity for observing contingent compared to mirrored movement patterns. B. Plots illustrate corresponding contrast estimates obtained for the four stimulus categories for three different local maxima: left IPL (-48, -34, 42), right pSTS (54, -42, 8) and right IFG (56, 16, 6). Error bars represent standard errors. The principally activated voxels are overlaid on the mean structural anatomic image of the 21 male participants: $p < .05$, cluster-level corrected; L = left hemisphere; R = right hemisphere; IFG = inferior temporal gyrus; pSTS = posterior superior temporal sulcus; IPL = inferior parietal lobule.

The observation of videos where characters were moving with fluent compared to those with rigid kinematics did not reveal any differential neural response. This confirms our hypothesis that there is no biological bias for the AON, possibly because the humanoid appearance of the agents contextualizes their action goals. We argue that a movement analysis with respect to goal-intentionality may take place in order to enable the observer to represent the agents' intentions in a social context but that this does not require a tight kinematics match. The opposite contrast, investigating the perception of rigid vs. smooth kinematics revealed activations in regions of the SNN, namely the left inferior frontal gyrus (IFG, pars triangularis), the left angular gyrus, corresponding to the left TPJ, as well as bilaterally the dorsal medial prefrontal cortex (dmPFC; see Fig. 7). We assume that a mismatch between the expectation with respect to the agents' biological nature on the one hand and the nonbiological kinematics of their movements on the other prompts inferences about the intentions behind the agents' actions.

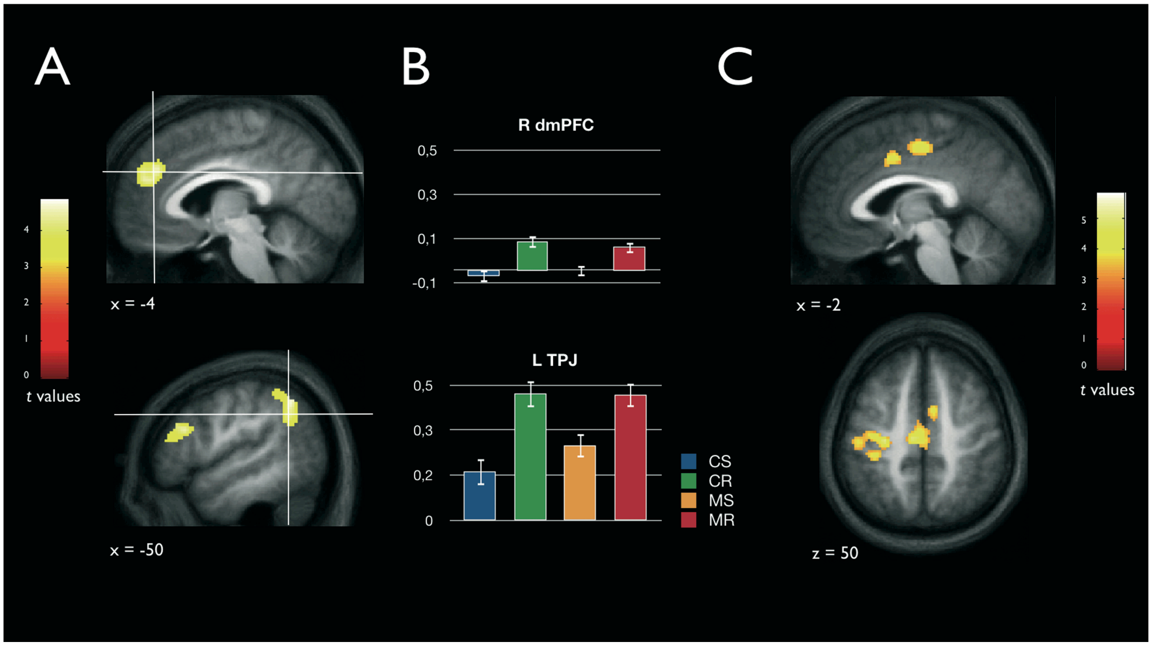

Figure 7. Neural Results of Study 3: Effects of Movement Fluency. A. Regions of the SNN associated with the observation of videos with rigid compared to smooth movement velocity. B. Plots illustrate corresponding contrast estimates obtained for the four stimulus categories for two different local maxima: right dmPFC (10, 46, 28) and left TPJ (-42, -56, 40). Error bars represent standard errors. C. Interaction effect evaluating brain regions more responsive to contingent than to noncontingent videos when the motion was biological, than when it was nonbiological. The principally activated voxels are overlaid on the mean structural anatomic image of the 21 male participants: $p < .001$, cluster-level corrected; extent threshold: 10 voxels; L = left hemisphere; R = right hemisphere; TPJ = temporo-parietal junction; dmPFC = dorsomedial prefrontal cortex.

4 Study 4: Generating Mental State from Animacy Cues in High-Functioning Autism

4.1 Theoretical Background

4.1.1 The Relevance of Animacy for Social Cognition

“Animacy” is a term denoting the perception of other entities as sentient or alive beings (Santos et al., 2008). The ability to discriminate between animate and inanimate things appears early in development (e.g. Gelman et al., 1995) and seems to be universal (Barrett, Todd, Miller, & Blythe, 2005). Thus, inferring intentionality from perceived movement can be used as an empirical indicator for animacy (Santos et al., 2008).

Interestingly, the attribution of intentionality to moving entities does not necessarily require an organism-shaped body (ibid.). In the early 1950s, William Grey Walter designed two autonomous mobile robots, Elmer and Elsie, that were equipped with a light source and sensor and that were programmed to explore their environment, avoiding obstacles in search of other light sources. Given these settings, when placed together in a room, the two robots displayed a cycle of highly coordinated behavior by oscillating around each other. Walter noted that “Crude though they are, they (the robots) give an eerie impression of purposefulness, independence and spontaneity” (Walter, 1950; p.45).

An elegant paradigm for the investigation of animacy perception from watching nonbiological agents has been introduced by Heider and Simmel (1944). The researchers used silent videos of moving geometric shapes, where one object either followed another and/or reacted to its movements. Despite their nonbiological appearance, the two objects were ascribed human qualities and the resulting interactive movement patterns were defined as social encounters. Santos and colleagues (2008) for example, looked further into the specific kinematic factors that would influence animacy perception and found that animacy experience increased with the time a moving object paused in the vicinity of a second object and with increasing complexity of interaction between the objects (approach and responsiveness).

Thus, by identifying specific intentions and goals in movement patterns, observers may detect animacy from movement kinematics. Research using the Heider and Simmel (1944) or related paradigms was able to consistently demonstrate that observers make use of their implicit knowledge of social contingencies to judge social interactions and to attribute intentions, thoughts and desires to moving agents which are perceived as animate (Blythe et al., 1996; Rimé et al., 1985; Santos et al., 2010, 2008; Scholl & Tremoulet, 2000). In this line, it has been proposed that the ability to identify animacy is a prerequisite for ToM (Santos et al., 2008).

4.1.2 Neural Correlates of Animacy Perception

The above mentioned paradigm first introduced by Heider and Simmel (1944) was further developed and refined in order to better characterize the behavioral and neural correlates of animacy perception. Neuroimaging studies were able to attest the involvement of the brain regions related to different aspects of social cognition, hence further corroborating the idea that the ability to detect animacy is related to social cognition (for a review see Heberlein, 2008). Indeed, all brain areas which have been recruited by animacy perception are key regions of the SNN, namely the pSTS and the FG associated with social perception, the amygdala and the insula associated with processing of salient and affective stimuli and the TPJ, the dmPFC, the mOFC and the TP associated with mentalizing and evaluative processing (Castelli et al., 2000; Gao, Scholl, & McCarthy, 2012; Gobbini et al., 2011; Santos et al., 2010; Schultz et al., 2005, 2004; Schultz et al., 2003; Tavares et al., 2008).

4.1.3 Animacy Perception in Individuals with High-Functioning Autism

During development, humans acquire a large set of nonverbal skills and the intuitive knowledge to use them during social interactions. This enables them to develop a sense of reciprocity with others in order to successfully coordinate their actions and to communicate effectively. However, as already mentioned in the introduction (chapter 1.4) and chapter 2.1.3, HFA is characterized by difficulties with social interaction, both from a participant and from an observer perspective.

Indeed, animacy perception tasks using two interacting shapes have shown group differences with regard to the frequency of interpretations referring to mental states between individuals with HFA and controls, despite comparable performance on explicit ToM tasks (Abell, Happé, & Frith, 2000; Klin, 2000) and preserved skills in physical attributions (Klin & Jones, 2006). A recent study used animacy displays of two moving dots which were derived from videos of real humans interacting, as well as a forced choice task asking participants to categorize patterns of Chasing, Fighting, Flirting, Following, Guarding and Playing (McAleer, Kay, Pollick, & Rutherford, 2011). The authors have found a comparable performance between HFA and control group in terms of accuracy and response patterns (ibid.). However, this task removed the need for mentalizing and solely investigated intention understanding. Recognition of action or intention (as opposed to that of affect or Theory of Mind) has been found to be intact (Abell et al., 2000). Paralleling these difficulties, individuals with HFA showed less pronounced neural responses in the STS, TPJ, dmPFC, amygdala, temporal pole and fusiform gyrus in response to animated stimuli as compared to controls (Castelli et al., 2002).

4.2 Experimental Design and Hypotheses

Interestingly, Congiu, Schlottmann and Ray (2010) have found that animacy prompts were able to amplify animacy attributions in autistic children. Similarly, Rutherford, Pennington, and Rogers (2006) showed that children with autism did not differ in animacy judgements after a training phase. These findings suggest that animacy perception might be preserved in autism, even if it is not used automatically and autistic persons may overcome their animacy perception deficit strategically. In order to investigate this, a paradigm is needed which allows i) parametric induction of animacy and ii) the investigation of both perception and experience of animacy.

A parametric task would be able to induce a continuous increase in the experience of animacy. Such a task would be most suitable for exploring the relationship between animacy attribution and mentalizing processes (Santos et al., 2008). A task that allows inducing a continuous graduate increase of animacy perception, could provide a sensitive measure in HFA (ibid.).

The experimental design of **study 4** was developed by Santos and colleagues (2008) and validated in an fMRI study by Santos and colleagues (2010). The stimuli consisted of short video clips displaying two spheres (see Fig. 8). The movement of sphere 1 was either continuous without any changes in direction, or contained an interruption followed by an approach towards the other sphere (approach). Sphere 2 either remained static or moved towards sphere 1 (responsiveness). These movement characteristics, approach and responsiveness, were modulated in a 2 by 2 design resulting in four possible stimulus categories, resulting in an increasing amount of objective animacy: 1) no approach/no responsiveness; 2) no approach/responsiveness; 3) approach/no responsiveness; and 4) approach/responsiveness. Participants were instructed to watch each video and rate the "person-likeness" of each scenario.

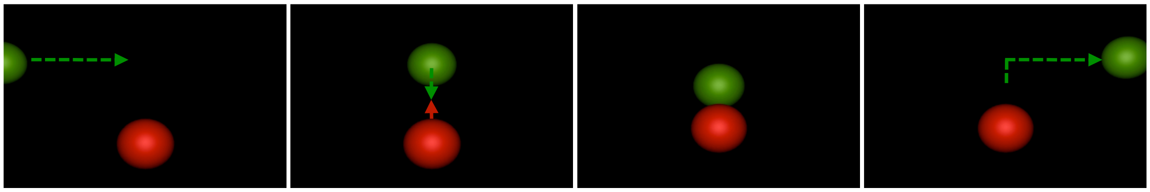

Figure 8. Sample Stimuli of Study 4. Four frames extracted out of a stimulus video clip containing approach and responsiveness with arrows indicating the pathways of movements.

Study 4 compared a group of 13 adults with HFA (mean age: 29.08 ± 4.33 years) with 13 matched controls (mean age: 29.77 ± 4.02 years). By using a more sensitive measure for animacy perception, the study aimed to provide empirical support of the assumption that individuals with HFA may use different cognitive strategies when processing social information.

We contrasted the two groups with regard to increasing objective and subjective animacy. The objective animacy measure investigated brain regions whose activity correlated with the perception of increasing stimulus complexity. The subjective animacy measure investigated the activity of which brain areas correlated with increasing ratings of “person-likeness”. Because HFA show preserved skills for physical attributions (Klin & Jones, 2006), as well as for intention attributions but not for mental states attribution (McAleer et al., 2011), the applied cognitive strategies might rely more on physical properties of the stimuli. This, may result in a comparable performance in animacy detection but different subjective experience between the two groups (Kuzmanovic et al., 2011; Piggot et al., 2004). Thus, we hypothesized that HFA and controls would differ with regard to the subjective animacy experience, but not with regard to objective animacy perception.

4.3 Findings and Conclusions

Study 4 replicated the increasing recruitment of the SNN for both increasing subjective and objective animacy in typically developing participants found by Santos and colleagues (2010). The neural activations included bilaterally the insula, the amygdala, the STG, the TP, the FG and the ventral and dorsal mPFC (significance threshold for fMRI group results: $pc < .05$ at the cluster-level, corrected for multiple comparisons and $p < .001$ at the voxel-level, uncorrected).

The behavioral results did not show a significant group difference in ratings of the four stimulus categories with regard to animacy. This indicates comparable behavioral performances between the groups in the experimental task. Neurally, increasing perception of animacy (objective measure) did not reveal any significant group differences. Both groups share a common neural correlate for perceiving increasing complexity in the stimulus material. This correlate, included regions of the SNN, namely the vmPFC and the bilateral STG. While the STG has been associated with the detection of animacy-inducing movement characteristics (Santos et al., 2010; Schultz et al., 2003; Wheatley, Milleville, & Martin, 2007), the vmPFC plays an important role in generating integrative, evaluative judgments

(Amodio & Frith, 2006; Zysset et al., 2002). We conclude that both groups were able to detect the physical features of the stimuli, and ascribe intentionality to them. Moreover, the common neural substrate of this performance seems to be related to perceptual analysis and its evaluation. In contrast, when regarding the subjective animacy measure, we found a significant group difference, namely that the bilateral activity in insula, STG, TP, amygdala and dmPFC was correlated more strongly with increasing ratings of animacy in controls than in HFA (see Fig. 9). This corroborates previous findings showing that the neural mechanism involved in the processing of animate stimuli does not recruit neural regions implicated in mental inference in the HFA group (Castelli et al., 2002; Schultz et al., 2003) as a result of reduced modulation of subjective experience by increasingly social stimuli.

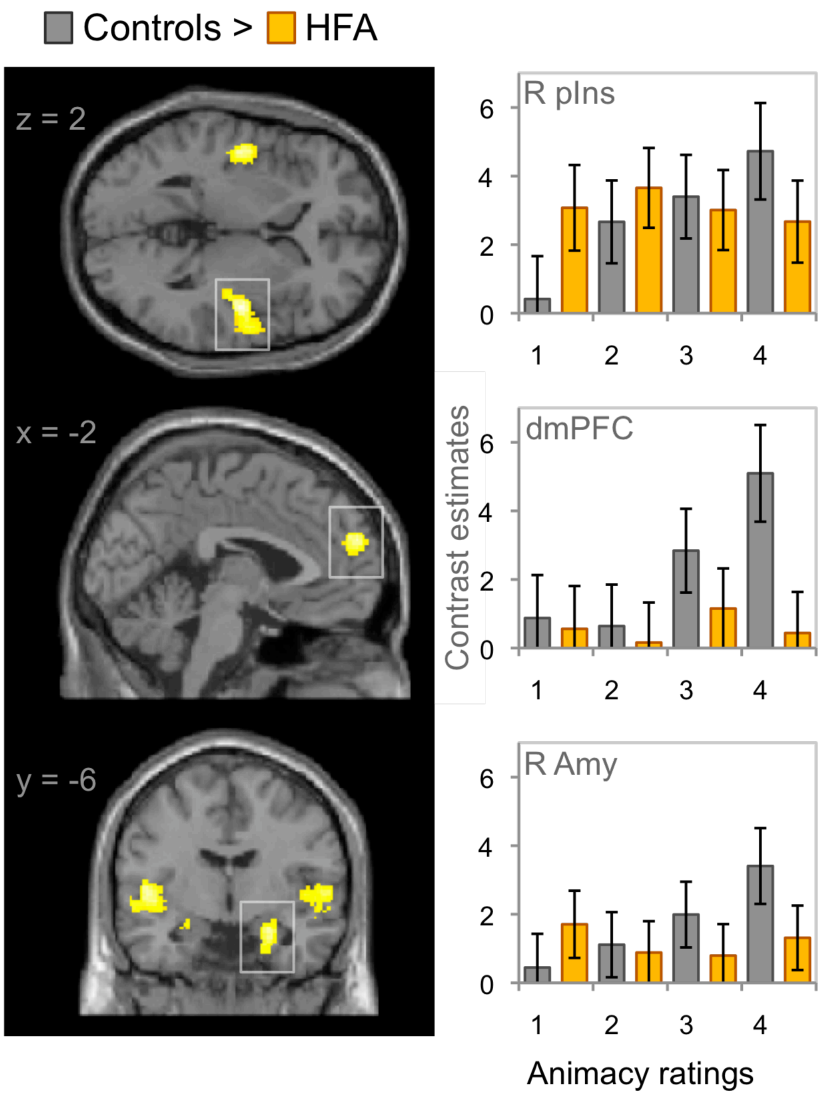

Figure 9. Neural Results of Study 4: Subjective Animacy Experience. Within-subject correlations between the BOLD signal and the subjective animacy (as indexed by participants' event-related ratings) that were significantly greater in the control than in the HFA group. Activation maps show group differences in the parametric modulation of the general neural response to stimuli by subjective animacy and the plots show the corresponding contrast estimates for the four levels of subjective animacy, in the following activation peaks: R pIns: x=46, y=-12, z=2; dmPFC: x=-2, y=58, z=24; R Amy: x=24, y=-6, z=-18. , The contrast estimates were derived from a supplementary 4 x 2 categorical model including regressors for each response option, separately for the two groups. R, right; p, posterior; Ins, Insula; dmPFC, dorsomedial prefrontal cortex; Amy, Amygdala.

Taken together, these results indicate dissociable cognitive strategies applied during an animacy judgement task. Thus, we provided for the first time empirical evidence for the hypothesis, that feature-based processing of social stimuli is intact in HFA, but that there is no modulation of subjective responses to these stimuli that relate to mind attribution and increased salience. This corroborates the findings from **study 2**, and supports the assumption that in HFA the search for meaning within a social environment is guided more strongly by rule-based computations than by motivational predisposition to spontaneously respond to social stimuli.

5 General Discussion

The findings of each of the four studies presented in this dissertation have already been discussed in their respective chapters (2.3, 3.3, 4.3). However, this section will embed the current findings into a larger context of previous research and discuss how they extend current knowledge in this field (chapters 5.1-5.4). Finally we will talk about some of the limitations of the paradigms (chapter 5.5).

5.1 Virtual Characters as a Tool for Nonverbal Research (Studies 1-4)

In the introduction (chapter 1.2) we mentioned that the investigation of nonverbal behaviors is confronted with several methodological problems, which make it hard to capture and very difficult to control experimentally. Humans are highly attuned to perceive even slight variations both in appearance and movements of social others (Santos et al., 2008). Therefore, considering that nonverbal behaviors are highly context-dependent (Gary Bente et al., 2008) and both produced and perceived outside of awareness (Choi et al., 2005), the use of actors performing nonverbal movements may not be the most appropriate stimulus material, because it may be inaccurate and/or inconsistent.

Such methodological problems can be solved by using thin slices of the behavioral stream (Ambady & Rosenthal, 1992) and virtual characters (Vogeley & Bente, 2010). The use of samples of naturally occurring nonverbal behaviors, would ensure the inclusion of rich, complex nonverbal patterns that would carry implicit movement qualities, thus adding to the material's ecological validity (Ambady & Rosenthal, 1992). Using computer-generated virtual characters helps to create stimuli in which movement information is controlled independently from shape information. Apart from allowing to standardize agents' appearance by replacing them with 3D models, it has the advantage of systematic manipulability which allows the precise experimental manipulation of the action dynamics according to the conditions of interest (Vogeley & Bente, 2010). In the current studies we have made use of virtual characters and we were able to further corroborate the validity of this research tool for the investigation of nonverbal behavior in a neuroimaging context.

For example, in the study of social gaze (**study 1** and **study 2**) the systematic modification of facial characteristics for the generation of the virtual stimulus faces provided an effective countermeasure for confounding influences such as face morphology and non-intended mimicry movements (Kuzmanovic et al., 2009). Interestingly, Bailenson, Blascovich, Beall and Loomis (2001) have demonstrated that people assign sentience to a virtual character, especially when that character exhibits realistic gaze behavior. Thus, in order to increase their ecological validity, we included an eye blink in the gaze behaviors of the virtual faces. We found that this indeed had a positive effect on ecological validity as confirmed by the post-scanning questionnaires. Our findings corroborate previous research, which shows that virtual characters are able to elicit the percept of presence and a broad range of responses in a human observer. And yet, while they do so, they may also be a more comfortable type of stimulus material for individuals with HFA to be exposed to during experimental investigations (Parsons & Cobb, 2011).

In **study 3** we used full-body humanoid standardized virtual characters and thin slices of the behavioral stream captured from real-life interactions. This stimulus material was developed based on 10 videos, filmed at the University of Cologne, originally lasting for 3 minutes and depicting dyadic role-play interactions between two seated individuals. Silent animations were subsequently created using the keyframing technique and the commercially available character animation software Alias MotionBuilder 7.5. This was done by transcribing the movement protocols from the original video recordings into virtual space onto two anonymous standardized virtual characters. This transcription process is described in detail by Bente and colleagues (2008). We chose to map the movements onto virtual characters resembling wooden mannequins instead of using point-light displays (PLDs), since the latter may not be as appropriate when studying the effects of more complex motion information, as is the case of full-body nonverbal behaviors. Hodgins, O'Brien and Tumblin (1998), for example, argue that subtleties of the motion are less perceptible when sparse graphical models such as PLDs or stick figures are used and have found that subjects are better able to discriminate motion variations with a fully rendered (polygonal) character. Chaminade, Hodgins and Kawato (2007), however, found that sensitivity to different motion types is only affected by the simplest rendering style (PLDs) but not by a range of fully rendered characters, including an ellipsoid model, similar to the mannequin model used in **study 3**. Similarly, McDonnell, Jörg, McHugh, Newell and O'Sullivan (2008) have shown in a study that included among other virtual characters a mannequin model, that the perception of emotional actions is highly robust and to the most part independent of the character's body. Still, the neutral mannequin was preferred to a detailed full character, because when more detailed models are used, subtle flaws in rendering, body shape, posture, or expression may draw attention to appearance from motion and the characters are in danger of entering the uncanny valley (Mori, 1970). The uncanny valley states that the more human a robot or virtual character looks like, the more likely it is that subtle imperfections are to be perceived as strange. In fact, in our **studies 1 - 3** we made use of anthropomorphic virtual characters, shown either as faces or full-bodies. Such characters have realistic human features but can still being easily recognized as artificial. We therefore conclude that we successfully managed to avoid the uncanny valley phenomenon in our stimuli.

Finally, **study 4** made use of simple geometric shapes (two spheres) which were able to give rise to rich percepts of animacy and intentionality just by abiding with certain spatiotemporal characteristics (approach from one sphere to the other and responsiveness from the addressed sphere to the actively moving sphere). The systematic manipulation of these factors allowed us to create a parametric variation in the degree of the complexity of movement patterns which would otherwise not have been possible. It also allowed us to exclude top-down influence of anthropomorphizing humanoid shapes due to the nonbiological appearance information.

5.2 The Contribution of Spatiotemporal Movement Characteristics to the Processing of Nonverbal Behavior

5.2.1 Gaze Duration as a Dynamic Aspect of Social Gaze

Gaze behavior is critical in everyday interaction. It can be considered a deictic cue, and can be used to direct the attention of another person to an object (Pfeiffer, Vogeley, & Schilbach, n.d.). Conversely, by following other persons' gaze we gain access to their attentional focus, which is essential for understanding their mental states (ibid.). Moreover, infants spontaneously follow another's gaze only if the gaze shift is preceded by direct eye contact, hence suggesting that social gaze may have an ostensive value (Csibra & Gergely, 2006; Gergely & Csibra, 2003). This, in turn, explains why it plays a major role in early social development as a precursor for ToM (Emery, 2000). Such findings demonstrate that there is a lot of subtle complexity in the way gaze is used in order to coordinate behaviors and interact with other people. In particular, time parameters of gaze behavior such as duration seem to be of great importance. Gaze duration is a much less investigated aspect of social gaze compared to gaze direction (Foa et al., 1981; Georgescu et al., n.d.; Kuzmanovic et al., 2009).

Our paradigm is the first to investigate temporal aspects of gaze behavior in a neuroimaging context and shows an innovative finding as it is able to disentangle effects of salience detection on the one hand and evaluation of gaze cues on the other. Moreover, although atypical processing of social gaze in HFA is thought to reflect an impairment in understanding the intentional nature of gaze cues, little evidence has emerged in the form of atypical engagement of the SNN network during gaze perception (Hagen et al., 2013). Our parametric manipulation of increasing gaze duration (1s, 2.5s and 4s) was indeed able to increase the feelings of self-reference and communicative intent perceived in the stimulus material, as confirmed by post-scanning questionnaires of the typically developing group. This is mirrored on a neural level, by the involvement of the mPFC in the perception of increasing direct gaze duration, a key region of the SNN.

5.2.2 Movement Fluency and Contingency as Dynamic Aspects of Movement

The detection of meaning in social stimuli can be based either on kinematic properties of the motion itself or on kinematic properties of movement patterns between objects (Blakemore et al., 2003; Santos et al., 2008). The investigation of nonverbal communicative dyadic interactions may help clarify the role of these two factors in social perception, a question which had not been asked hitherto. Thus, fir the first time, **Study 3** used humanoid virtual characters moving smoothly or rigidly and either engaged in reciprocally contingent or perfectly synchronous interactions. We found that social communicative dyadic interactions are perceived as more plausible and natural, when there is reciprocity in the contingent movement patterns and, to a lesser extent, also when the movements follow a smooth rather than a rigid velocity profile. Our operationalization of contingency seemed to have a greater influence on the naturalness judgments than movement velocity, most likely because it involved the most obvious manipulation. **Study 4** used non-anthropomorphic geometric shapes to show that the complexity of contingent movement patterns (via systematic manipulation of approach and responsiveness characteristics) increases the perception of animacy. These findings are mirrored on the neural level by the activation of the two neural networks involved in ascribing meaning to movement cues, namely AON and SNN.

5.3 The Involvement of the AON and SNN in the Perception of Meaning from Movement Cues

The AON has been found to be activated when a kinematic analysis of movement cues is performed in order to decode intentionality. On the other hand, the SNN is engaged by tasks which require participants to consciously deliberate on the intentions of observed agents, for example when observed actions have an unusual goal, are implausible or inconsistent with the context (Brass et al., 2007; de Lange et al., 2008; Keysers & Gazzola, 2007; Santos et al., 2010; Spunt et al., 2010; Thioux et al., 2008; Uddin et al., 2007; Van Overwalle & Baetens, 2009).

It has been proposed that the two systems might interact, since the anterior and posterior nodes of the SNN and AON share direct connections (Uddin 2007). Although the exact nature of the interactions between the two networks is unknown, it is likely that the connectivity between them facilitates the integration of information that is necessary for processing social cues. Nevertheless, the exact relationship between SNN and MNS is complex and the ways in which the two might contribute independently and interact to influence social perception are still to be explored. Indeed, much of the debate in social cognition might result from choosing tasks that isolate the processes of just one neural network (Keysers & Gazzola, 2007). However, it is essential to start designing tasks that reflect the complexity of social life to test how the social brain forms an integrated whole. Nonverbal communicative interactions are indeed a rich source of such complexity and would thus be appropriate stimulus material to work with.

Our results confirm that the AON is involved in processing all types of movement cues but additionally show that it is not modulated by movement velocity. However, perceiving two bodies engaged in contingent interaction patterns does elicit more AON activation than watching two bodies in perfect synchrony. This may be the case because it is more challenging to represent the reciprocity of the actions of two agents rather than those of two actors performing simultaneously the same movements. Confirming previous research, we were able to show that the SNN is only engaged when an implausible action is presented and that this implausibility can be defined by an incongruency between previous beliefs about the nature of the agent and the velocity of their movements. If an agent looks human but moves jerky and robotic, people are more likely to deliberate on the reason for their implausible behavior. Interestingly, the SNN was not involved in perceiving contingent compared to synchronous movements as previous studies suggested might be the case (e.g. Centelles et al., 2011). However, we believe that this is linked to the task of the present study, in which participants were asked to judge the naturalness of the scenes, which likely stimulates intuitive evaluation processes. They were neither asked to judge the social content of these interactions nor to infer their mental states or feelings. Thus, intuitive evaluations, compared to deliberate and reflective ones, do not rely on the integration of a wide range of social information and decision-making processes and rather trigger a pre-reflective simulation process via the AON (Georgescu et al., 2013).

Our findings are in concert with recent research has shown that under specific conditions both networks might be needed to catch the social intentions carried by whole-body motion (Centelles et al., 2011). To infer another person's intentions, we need to complement sensorimotor knowledge with conceptual information about mental states and attitudes (Mitchell, Heatherton, & Macrae, 2002). Therefore, kinematic analyses via the AON and mentalizing processes via the SNN are not mutually exclusive. (Spunt et al., 2011) conducted the first study to simultaneously manipulate and measure the level of action identification during the observation of ordinary human actions performed in natural contexts. They showed that regions of the AON are involved at all levels of the identification task but that the SNN is associated with mentalizing observed actions. Thus the AON might be involved, as a more general and early stage of processing, in the understanding of a wide range of actions rather than sustaining the perception and interpretation of social movement cues which is the functional role of the SNN (Santos et al., 2010). Study 3 corroborated for the first time this hypothesis on AON and SNN activity in the context of observing nonverbal communicative interactions.

5.4 Perturbations of Nonverbal Processing in High-Functioning Autism

In the introduction chapter (chapter 1.4) we have stated that individuals with HFA have problems in decoding nonverbal behaviors (Uljarevic & Hamilton, 2013) and in relying on nonverbal behavior to make person judgments (Kuzmanovic et al., 2011; Schwartz et al., 2010). Neuroimaging studies have demonstrated that the processing of gaze cues, like gaze direction, for example, has been found to by atypical in HFA (Hagen et al., 2013; Pitskel et al., 2011). Studies investigating the perception of the social contingencies in an interaction context also show atypical activation in this network (Castelli et al., 2002; Schwartz et al., 2010). Interestingly, it has been suggested, that social cognition deficits in HFA may not be based in the perception of social cues per se, but result from an impairment to extract relevant information from these cues necessary for social communication (Nation & Penny, 2008; Pelphrey et al., 2005; Ristic et al., 2005; Senju & Johnson, 2009a). Thus experimental designs are needed that allow us to characterize what exactly is atypical in HFA, social perception or a more high-level processing (e.g. the detection of communication intent) and what mechanisms subserve an atypical response to social stimuli.

The design of **Studies 2 and 4** allowed us to target this question. **Study 2** shows that gaze processing deficits are not based in eye gaze discrimination per se or in social perception in general. Thus social processing is to a certain degree intact in HFA. Moreover, our results extend previous research findings by showing that the deficits in social cognition in HFA seem to be related to the evaluation and interpretation of cues, and the use of such cues to understand the intentions and mental states of other people. In addition, **Study 4** shows that, despite the fact that the perception of nonverbal cues may be comparable to that of typically developed individuals in both behavioral and neural measures, ascribing meaning to a stimulus may rely on a different cognitive strategy for individuals with HFA.

5.5 Limitations of the Various Paradigms

Nevertheless, the current thesis is also limited in the interpretation of results, due to methodological aspects and operationalization of constructs.

First, the experimental design of **studies 1 and 2** has two limitations: i) the direct gaze conditions constituted ¾ of all events, and ii) the direct gaze conditions included an additional gaze shift compared to the averted gaze condition. Both of these factors could have rendered the direct gaze stimuli more salient irrespective of the gaze behavior per se. Thus, the activation of the SNN could be elicited by different factors in the two participant groups: by an effect of novelty for the averted gaze condition in HFA and by an effect of increased motion quantity in the control group, as reflected by the increased pSTS and MT/V5 activation, two motion-sensitive regions of the brain. A way of avoiding such a confound in the future would be to use a neutral starting point for all videos (e.g. looking upwards) and a face with closed eyes as a control condition (instead of averted gaze, which is a manipulation of direct gaze).

Second, if noncontingency would have been operationalized differently in **study 3**, this could have revealed a different set of findings. For example, instead of mirroring the actions of one agent, we could have time-lagged their actions. In such case, the contrast between contingent and noncontingent interactions might not engage brain networks differentially, because viewers would interpret a relationship among people moving simultaneously on screen (Iacoboni et al., 2004), even when their behavior is not mutually oriented. This is due to the fact that social contingencies in communicative interactions are complex and characterized by high levels of variability and noise (Cappella, 1981). Indeed, human adults tend to interpret and verbally report social experiences as a series of causally linked events (Tenenbaum & Griffiths 2003).

Third, **study 3** used humanoid virtual characters in all videos to investigate different movement parameters. However, research has shown that factors of kinematics and appearance can interact (Cross et al., 2011; Saygin et al., 2011; Shimada, 2010). Anthropomorphism and belief about the biological identity of a stimulus have been known to facilitate motor resonance, a cognitive process known to involve regions of the AON (Chaminade et al., 2007; Stanley, Gowen, & Miall, 2007). Moreover, it has been known that top-down factors like appearance and belief about animacy modulate SNN engagement (Chaminade et al., 2012, 2007; Krach et al., 2008). Therefore, by using only humanoid characters and by informing the participants that the scenes they were watching were based on original live-action videos, participants assumed that the nature of the movements they were watching was human. While our paradigm allowed us to investigate movement information independent of appearance information, we did not manipulate appearance information to achieve a balanced design and cannot rule out the top-down influence of appearance information on the processing of movement cues. We can however state that the influence was kept constant over all conditions and that we investigated movement cues in non-humanoid shapes in another study, namely **study 4**.

Fourth, the interpretation of the results in **study 4** is limited due to the nature of the paradigm itself. While the novel parametric task developed by Santos and colleagues (2008) is able to induce a continuous increase in animacy judgments, there is a confound in the stimulus material: Indeed, increasing interactivity of the two spheres is confounded with increasing complexity of their movement patterns. Despite the fact, that complexity is indeed an intrinsic quality of interactivity, it would be interesting if future studies would try to disambiguate the contribution of these two factors to the perception of animacy.

Finally, we would like to stress the necessity of using eye-tracking systems for future social neuroscience investigations, especially for paradigms on the observation of dyadic social interaction. Such systems enable the control of whether participants are compliant regarding the instructions and whether they focus their attention on the stimulus material. Moreover, without eye-movement monitoring, it could be argued that the differences in neural activation might result from imbalanced eye movements in one condition rather than another, and this differential eye movement might be related to a participant's experience with the task. Especially paradigms focusing on contingency factors and the observation of dyadic interaction would need eye-tracking to explore more in depth what features of these complex scenes are attended to at which times exactly.

6 Conclusion

Being able to accurately decode nonverbal behaviors is essential for human communication. However, meaningful information is not only conveyed by static cues, which have already been extensively investigated in the past, but also by subtle movement dynamics. Investigating such subtle movement dynamics opens up new avenues for the investigation of social cognition in healthy and psychopathological contexts. Thus, this thesis investigated the correlates of perceiving and processing dynamic nonverbal social cues in the human brain using fMRI along with behavioral methods.

First, we demonstrate the utility and validity of several digital simulation paradigms for nonverbal behavior research in a neuroimaging context. Further, we show for the first time that the observation of nonverbal communicative interactions is modulated by different spatiotemporal factors of perceived movement and that this is associated with both the AON and the SNN. In addition, we contribute to an ongoing debate by showing that in the context of the observation of complex human interactions, there is no biological bias of the AON. Furthermore, we demonstrate for the first time the domain-specificity of the two neural networks AON and SNN in the context of observing complex human interactions. Finally, we demonstrate that HFA is associated with deficits in social processing more so than social perception, but that social perception may rely on other cognitive strategies compared to typically developing individuals.

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