Social cognition and nonverbal behavior: lessons from neuroimaging and high-functioning autism

Inauguraldissertation
zur
Erlangung des Doktorgrades
der Humanwissenschaftlichen Fakultät
der Universität zu Köln
nach der Promotionsordnung vom 10.05.2010
vorgelegt von

BOJANA KUZMANOVIC

aus

Prnjavor, Bosnien und Herzegowina

März, 2012

Diese Dissertation wurde von der
Humanwissenschaftlichen Fakultät
der Universität zu Köln
im Juni 2012 angenommen.

Primary supervisor: Prof. Dr. Gary Bente

University of Cologne
Department of Psychology
Gronewaldstraße 2
50931 Cologne, Germany

Secondary Supervisor: Prof. Dr. Dr. Kai Vogeley

University Hospital Cologne
Department of Psychiatry and Psychotherapy
Kerpener Straße 62
50924 Cologne, Germany

Acknowledgments

I would like to thank my supervisors, Gary Bente and Kai Vogeley, who intensively and comprehensively supported me by providing extensive knowledge, warm, esteeming and respectful working atmosphere, and great experiences both within the home-lab and the international scientific exchange that maximized excellence and creativity of the present work. Furthermore, I would like to thank Dieter Sturma for appreciating my work and offering exciting future perspectives. Many thanks to countless colleagues from the University Hospital Cologne, Research Center Juelich and Max Planck Institute, who, beyond scientific expertise also demonstrated team spirit and kindness. From the first days as a student assistant greatly supervised by Silke Lux, through the bumpy road of never ending questions and doubts debated with patient fellows such as Simon Eickhoff, Ralph Weidner, Leonhard Schilbach and Alexandra L. Georgescu, up to recently met Jan-Hendrik Heinrichs and Anneli Jefferson, I have to thank many for contributing to my fascination for and progress within the research.

A special thank goes to the best sister Ana Truter and to Astrid Gawronski, my precious friend and fabulous colleague. This work is dedicated to my parents.

Table of Contents

1 List of experimental studies

Published (content-related ordering):

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.

Study 2: Kuzmanovic, B., Schilbach, L., Lehnhardt, F.-G., Bente, G., & Vogeley, K. (2011). A matter of words: Impact of verbal and nonverbal information on impression formation in high-functioning autism. *Research in Autism Spectrum Disorders, 5*, 604–613.

Study 3: Kuzmanovic, B., Bente, G., von Cramon, D. Y., Schilbach, L., Tittgemeyer, M., & Vogeley, K. (2012). Imaging first impressions: Distinct neural processing of verbal and nonverbal social information. *Neuroimage, 60(1), 179-188.*

Study 4: Santos, N. S., Kuzmanovic, B., David, N., Rotarska-Jagiela, A., Eickhoff, S. B., Shah, J. N., Fink, G. R., Bente, G., & Vogeley. K. (2010). Animated brain: a functional neuroimaging study on animacy experience. *Neuroimage, 53*(1), 291-302.

Under review:

Study 5: Kuzmanovic, B., Schilbach, L., Georgescu, A. L., Kockler, H., Santos, N. S., Shah, J. N., Bente, G., Fink, G. R., & Vogeley. K. (under review). When seeing does not lead to feeling: Absent neural responses to increasing animacy judgments in high-functioning autism. *Social Cognitive and Affective Neuroscience*.

1.1 Own contributions to experimental studies

Study 1: B.K. designed the experimental paradigm, collected the data, conducted the statistical analyses, prepared the first version of the manuscript and implemented the comments of co-authors and reviewers into the final version of the manuscript. The completion of the experimental paradigm and the data collection were part of diploma thesis by B.K., while the rest of the work was conducted within the doctoral thesis preparation.

Studies 2-3: B.K. designed the experimental paradigm, collected the data, conducted the statistical analyses, prepared the first version of the manuscript and implemented the comments of co-authors and reviewers into the final version of the manuscript.

Study 4: B.K. conducted the statistical analyses, wrote the statistical analysis and results section of the manuscript and commented the manuscript draft.

Study 5: While using the experimental design by Natacha S. Santos, B.K. collected the data, conducted the statistical analyses, prepared the first version of the manuscript and implemented the comments of co-authors and reviewers into the final version of the manuscript.

2 List of abbreviations

Brain regions:

ACC	anterior cingulate cortex (1)
dmPFC	dorsomedial prefrontal cortex (2)
FFG	fusiform gyrus (5)
mPFC	medial prefrontal cortex (1-4)
mOFC	medial orbitofrontal cortex (3)
PaCC	paracingulate cortex (4)
PC	precuneus (6)
PCC	posterior cingulate cortex (6)
pSTS	posterior superior temporal sulcus (7)
STG	superior temporal gyrus
TP	temporal pole (8)
TPJ	temporoparietal junction (9)

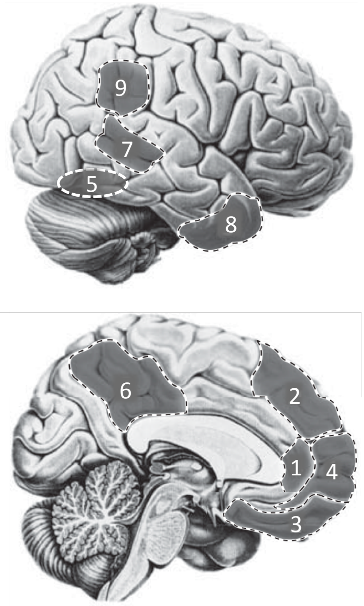

Fig. 2.1 Anatomical locations of abbreviated brain region labels. Adapted from Lieberman, 2010.

Other:

BOLD	blood oxygenation level dependent
fMRI	functional magnetic resonance imaging
HFA	high functioning autism
SoE	strength of evaluation
SOF	subjective-objective fit
ToM	theory of mind

3 General introduction

Social brain theory proposes that humans are equipped with sophisticated skills to detect, interpret and react to social stimuli in their environment in order to enhance their survival success (Dunbar & Shultz, 2007). When living in extended and complex social groups, these skills are essential when it comes to build and maintain relationships, understand and manipulate the intentions of others and convey information and knowledge. Thereby, the nonverbal communication and the interpretation of animated agents occur phylogenetically and ontogenetically earlier in the development than the verbal communication (Ambady & Weisbuch, 2010). Interestingly, these two domains of social information appear to rely on distinct cognitive and neural mechanisms differing in their quality and explicit availability but also tightly interacting with each other. Because of the special role of social information that is not transmitted via the semantically defined and syntactically logical language related to a more formal way of thinking, the present work focuses on neural correlates of the perception of nonverbal and animated social stimuli and their implications for social psychology.

The exceptional importance of being able to interact in the interpersonal and animated world characterized by uncertainty of meanings and outcomes becomes saliently recognizable in problems of individuals with high functioning autism (HFA) due to their specific deficits in social cognition (see 5.1.4 and 6.1.3). While being perfectly able to engage within defined rules of physical and logical coherences, individuals with HFA fail to attend to or to understand social cues such as a gaze or a smile in their everyday life (Klin & Jones, 2006; Klin, Jones, Schultz, & Volkmar, 2003). Investigating the neural processing of social and animated stimuli in HFA, thus, promotes a better understanding of this disorder and additionally enables a better specification of mechanisms underlying social cognition in healthy individuals.

The measurement of whole brain neural correlates of cognitive processes in the present work was carried out by functional magnetic resonance imaging (fMRI). With this hemodynamic-metabolic method, regionally specific information about relative neural activity is acquired non-invasively and indirectly, i.e. by making use of the blood oxygenation level-dependent (BOLD) effect based on differential magnetic properties of oxygenated and deoxygenated blood within a strong static magnet field combined with radio wave pulses and gradients (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 the present essay, studies included into the doctorial theses are summarized within three topics: Duration matters: the neural signature of the social gaze (**Study 1**), Distinct paths to first impressions via verbal and nonverbal information (**Studies 2** and **3**), and Different looks on animacy: mind attribution in high-functioning autism (**Studies 4** and **5**). The aim of the essay is to give an overview of research questions and findings for all studies in order to interrelate the theoretical backgrounds and arising conclusions to each other, while detailed information on methods and statistics is presented in the original articles attached in the appendix.

4 Study 1: Duration matters – the neural signature of the social gaze

4.1 Theoretical background

4.1.1 The role of gaze behavior in social cognition

Gaze behavior plays an important role in social interaction and communication. The gaze direction of another person indicates her focus of attention (Mason, Tatkow, & Macrae, 2005) and thus allows inferences about her mental states such as preferences and intentions (Simon Baron-Cohen, 1995), referred to as 'mentalizing' or 'theory of mind' (ToM, Frith & Frith, 2003). In turn, gaze shifts are also able to allocate the attention of an observer towards targets in the environment resulting in a 'joint attention' between two persons in reference to an object (Schilbach et al., 2010). Because of these relations to others' mental states, it has been suggested that gaze processing plays a fundamental role in the development of social cognition and that it is carried out by a specified operating system tuned to gaze detection and interpretation (Baron-Cohen, 1995; Senju and Johnson, 2009).

Particularly the direct gaze, i.e. the impression of 'being looked at', indicates that the perceiver has been noticed by others and thus signals a potential social interaction (Senju & Johnson, 2009). This self-referential character of the direct gaze and findings that infants and even newborns demonstrate a specific sensitivity to it on the neural and behavioral level (Farroni, Csibra, Simion, & Johnson, 2002; Hains & Muir, 1996) highlight its salience and its significance in social cognition. Direct gaze, as compared to averted gaze, has been demonstrated to modulate various aspects of cognitive processing: it was detected faster in a visual-search paradigm (von Grunau & Anston, 1995), and led to a greater attentional capture (Senju & Hasegawa, 2005), elicited facilitations in gender discrimination (Macrae, Hood, Milne, Rowe, & Mason, 2002), facial identity recognition (Hood, Macrae, Cole-Davies, & Dias, 2003; Smith, Hood, & Hector, 2006), and person memory (Mason, Hood, & Macrae, 2004) (but see Vuilleumier, George, Lister, Armony, & Driver, 2005), and had an advancing effect on likability and attractiveness ratings of others (Mason et al., 2005).

Importantly, not only the direction, but also the duration of the 'social gaze' is crucially informative within the context of person evaluation (Argyle & Cook, 1976). Increasing duration of direct gaze can enhance the impression of affiliation or threat, depending on context and extent of duration, and provokes increasing likability (Argyle, Lefebvre, & Cook, 1974), potency (Brooks, Church, & Fraser, 1986) and self-esteem (Droney & Brooks, 1993) ratings of target persons. Moreover, interpretation of the varying durations of gaze behavior seem to occur later in development as compared to the interpretation of gaze direction indicating that this parameter requires a more sophisticated processing (Einav & Hood, 2006; Montgomery, Bach, & Moran, 1998).

Taken together, gaze behavior opens up a unique access to investigate critical mechanisms in social cognition by means of manipulating its direction and duration in order to evoke distinct types of information processing.

4.1.2 Neural correlates of social gaze processing

The pivotal role of gaze behavior in many aspects of our everyday social life described above has promoted the interest in investigating neural correlates of gaze processing by using fMRI. One of the first insights provided by these studies regarded the demonstration of a brain region specifically associated with the perception of gaze shifts and other forms of biological motion. This region is located in the posterior superior temporal sulcus (pSTS) (Allison, Puce, & McCarthy, 2000; Pelphrey, Viola, & McCarthy, 2004; Puce, Allison, Bentin, Gore, & McCarthy, 1998), a multimodal area situated between the dorsal and the ventral visual stream recruited for actions towards objects and for object recognition, respectively (Hoffman & Haxby, 2000; Ungerleider & Haxby, 1994). Further research could demonstrate the involvement of the pSTS beyond the pure visual analysis, namely also in detecting gaze behavior that is indicative of certain intentions (Pelphrey, Morris, & McCarthy, 2004; Pelphrey, Singerman, Allison, & McCarthy, 2003).

A neural region that is more tightly related to inferences about mental states of others, and operates independent of visual analysis of biological motion is the medial prefrontal cortex (mPFC) (Amodio & Frith, 2006). However, in spite of greater self-referential significance of the direct gaze, the empirical evidence for stronger recruitment of the mPFC by direct as opposed to averted gaze remains controversial (Calder et al., 2002; Conty et al., 2007; George et al., 2001; Kampe et al., 2003; Wicker et al., 1998). Thus, whether more complex social cognitive processes and precisely which regions of the social brain network are involved or not seems to depend upon task demands and the general social context (Senju & Johnson, 2009; Vuilleumier et al., 2005).

4.2 Experimental design and hypotheses

Study 1 (Kuzmanovic et al., 2009) aimed to systematically provoke extended, evaluative social cognitive computations by incorporating the *duration* of direct gaze as an additional experimental factor (see Fig. 4.1). Previous neuroimaging research on gaze behavior focused on gaze *direction* only, thereby comparing faces that display direct and averted gaze. It neglected gaze duration that has been shown to crucially influence the social meaning of gaze (see 4.1.1). Therefore, in **Study 1** we implemented stimuli showing virtual characters with direct gaze of varying duration (ranging from 1 to 4 seconds, see Fig. 4.1A) and measured their likability using a four point-rating scale (ranging from very unlikeable to very likable) as well as their neural correlates. Specifically, we identified neural regions where the activity parametrically increased with increasing direct gaze duration by using fMRI. Different gaze durations were realized by employing dynamic video clips of 5.65 seconds length, with target faces initially displaying averted gaze, than shifting the gaze to the center for a varying time before finally returning to the initial averted position (see Fig. 4.1C). Additionally, all direct gaze events were also compared with stimuli displaying only averted gaze (see Fig. 4.1B). In consequence, we differentiated between two gaze-related effects on likability ratings and neural responses: i) simple comparison between direct and averted gaze; and ii) linear parametric modulation of neural activity associated with direct gaze processing by its duration.

While taking into account solely gaze direction may reveal processes related to *gaze detection*, modulation of direct gaze duration may be more prone to evoke refined self-referential and inferential thinking resulting in gradually varying person perception and neural responses dependent upon *gaze evaluation*. Thus, we hypothesized that *gaze direction* processing should be associated with social neural regions closely tied to biological motion analysis such as the pSTS, while higher-level social cognitive neural regions such as the mPFC should track direct *gaze duration* (see 4.1.2).

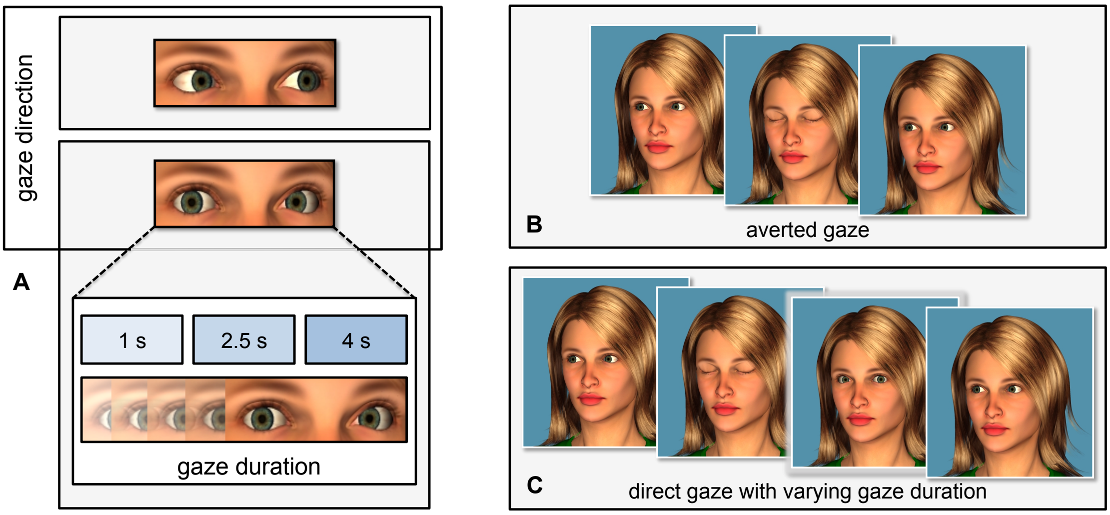

Fig. 4.1. Experimental design and stimuli from **Study 1** investigating the effects of gaze direction and gaze duration on likability ratings and neural processing. **A)** A schematic illustration of the experimental design focusing on the comparison between direct and averted gaze as well as on the effect of increasing direct gaze duration; **B)** an Example of a stimulus face displaying an averted gaze with a blink for reasons of ecological validity; and **C)** an example of a stimulus face displaying a direct gaze of varying duration (the highlighted picture) also including a blink within the shift from averted to direct gaze direction.

4.3 Findings and conclusions

Participants' ratings of stimulus faces revealed greater likeability for direct than for averted gaze ($p < .05$ for all pair-wise comparisons between averted gaze and direct gaze conditions, Bonferroni corrected), and a linear increase in likeability with increasing direct gaze duration (see Fig. 4.2C; significant main effect of direct gaze duration $F(2,42) = 3.66$, $p = .034$, and significant linear trend $F(1,21) = 5.84$, $p = .025$). Furthermore, fMRI analyses yielded distinct neural systems for processing the direction and the duration of interpersonal gaze: (i) the categorical comparison of direct and averted gaze, irrespective of varying duration of direct gaze, revealed activations in bilateral occipitotemporal regions including the pSTS (see Fig. 4.2A); (ii) whereas increasing duration of direct gaze evoked increasing activity in the mPFC including the anterior cingulate cortex (ACC), the paracingulate cortex (PaCC) and the medial orbitofrontal cortex (mOFC; see Fig. 4.2B; significance threshold for fMRI group results: $p_c < .05$ at the cluster-level, corrected for multiple comparisons and $p < .001$ at the voxel-level, uncorrected).

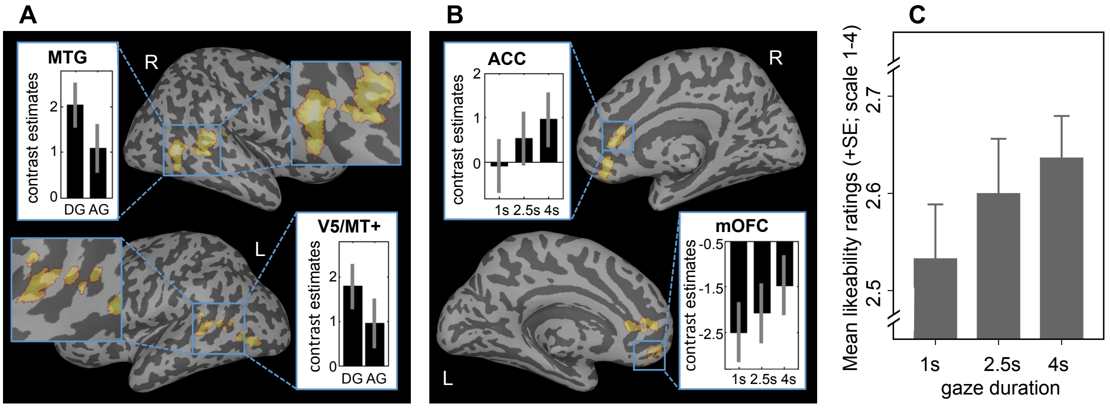

Fig. 4.2. Results from **Study 1** investigating the effects of gaze direction and gaze duration on likability ratings and neural processing. **A)** Main effect of the gaze direction showing stronger neural responses in bilateral occipitotemporal brain regions including posterior superior temporal sulcus for direct as compared to averted gaze; **B)** linear parametric modulation of the neural response to direct gaze by its duration: neural activity in the medial prefrontal cortex increased with increasing direct gaze duration; and **C)** main effect of direct gaze duration on likeability ratings of stimulus faces. L, left; R, right; MTG, middle temporal gyrus; V5/MT+, motion sensitive area; ACC, anterior cingulate cortex; mOFC, medial orbitofrontal cortex; error bars show 90% C.I..

These results indicate distinguishable cognitive mechanisms related to processing of gaze direction and gaze duration, respectively. The recruitment of the multimodal sensory area in the pSTS suggests that significant gaze direction changes are detected via complex visual analysis (Hoffman & Haxby, 2000; Puce et al., 1998). Beyond the pure decoding of gaze shifts (eye movements were present only in the direct gaze condition), direct gaze might have conveyed potential interpersonal intentions due to the self-referential social context that in turn led to more favorable likeability ratings and additionally triggered pSTS activity (Pelphrey, Morris et al., 2004; Pelphrey et al., 2003; Pelphrey, Viola et al., 2004). Supporting this interpretation, a recent neuroimaging study that realized the same amount of eye movement in conditions with eye shifts toward and away from the observer could demonstrate greater pSTS activation for direct gaze as well (Ethofer, Gschwind, & Vuilleumier, 2011). Importantly, however, categorically comparing direct and averted gaze resulted in neural responses that were restricted to occipitotemporal regions associated with sensory analysis, but did not include medial prefrontal areas involved in relatively more complex and sensory-independent social cognitive computations.

Conversely, varying direct gaze duration led to increases both in likeability ratings and in neural responses in the mPFC associated with diverse cognitive functions. These relate to monitoring the reward value and possible outcomes mediated by the mOFC (Amodio & Frith, 2006; Kringelbach, 2005), to person perception, mentalizing and self-referential processing consistently attributed to the PaCC (Mitchell, Banaji, & Macrae, 2005; Ochsner et al., 2005; Vogeley et al., 2001; Walter et al., 2004; Zysset, Huber, Ferstl, & von Cramon, 2002), and to online monitoring of emotional valence and of performance via error detection engaging the ACC (Bush, Luu, & Posner, 2000). Thus, the differential involvement of these areas indicates higher-order social cognitive processes related to decoding the ongoing communicational input and was paralleled by a positive effect of a prolonged gaze on impression formation.

In summary, while comparing different gaze directions reveals *detection* of self-referent significance conveyed by the direct gaze via visual analysis, varying direct gaze duration seems to require continuous *evaluation* in order to process possible interpersonal intentions and maintain adaptive outcome monitoring.

5 Studies 2 and 3: Distinct paths to first impressions via verbal and nonverbal information

5.1 Theoretical background

5.1.1 The importance of impression formation in social cognition

We are not treating all people equally and do not have the same expectations towards them. How much we trust others (Delgado, Frank, & Phelps, 2005), how much competence we ascribe to others (Gilbert & Krull, 1988; Rule et al., 2011) and even how we perceive others (Todorov, Gobbini, Evans, & Haxby, 2007) depends on impressions we form about them. Impression formation can be computed very explicitly and deliberately but also within few seconds and totally spontaneously (Uleman, Adil Saribay, & Gonzalez, 2008). In parallel to Watzlawick's idea that "one cannot not communicate" (Watzlawick, Bavelas, & Jackson, 1967), we cannot not form an impression of a social other we encounter, even if that means that we are not interested in him or her. Whether or not it results in specific personality traits such as being intelligent or generous, it always has a global valence in the sense that a target person is evaluated as rather positive or negative (Schiller, Freeman, Mitchell, Uleman, & Phelps, 2009). Irrespective of how we come to our impressions, they help us to predict others' behavior (Harris, Todorov, & Fiske, 2005; Rule et al., 2011), and influence our own behavior and further decisions towards others in various aspects of the everyday life such as personal relationships, or professional and political decisions (Frey, 1999).

5.1.2 Differences between verbal and nonverbal social information

Verbal and nonverbal social information differs in manifold ways leading to the assumption that the cognitive processes underlying its decoding may differ as well. On the one hand, verbal information is described as digital, with a clearly defined semantic code and a complex logical syntax enabling the transmission of elaborated and abstract contents (Kraemer, 2008). On the other hand, nonverbal social information does not have a clear semantic code and its complexity derives from multiple simultaneous cues (e.g., smile and gaze), which mutually influence each other's meaning (Bente &

Kraemer, 2008; Bente, Petersen, Kraemer, & de Ruiter, 2001; Bente, Senokozlieva, Pennig, Al-Issa, & Fischer, 2008; Kraemer, 2008). Furthermore, nonverbal cues are characterized by subtle dynamics extending in time rather than by static, isolated elements and are often produced and decoded outside awareness (Ambady & Weisbuch, 2010; Choi, Gray, & Ambady, 2005; Gilbert & Krull, 1988; Grammer, Honda, Juette, & Schmitt, 1999; Kraemer, 2008). Thus, it has been suggested that analog nonverbal cues have a stronger effect on affective relational level of interpersonal communication (Watzlawick et al., 1967). If these different domains of social information indeed trigger qualitatively different cognitive processes, than one should assume that the mechanisms that mediate impression formation based on verbal or nonverbal cues may also differ. In this case, critical implications can be deduced concerning interpersonal decisions in the public life requiring a certain degree of reasonability (Frey, 1999).

5.1.3 Neuroimaging background

A recent study has compared the processing of verbal and nonverbal social information in the context of an emotional state-judgment task (Zaki, Hennigan, Weber, & Ochsner, 2010). The findings support the assumption that these two domains are related to distinct neural systems. On the one hand, the processing of verbal information recruited the "mental state attribution system" including the dorsomedial prefrontal cortex (dmPFC) in the vicinity of the PaCC, precuneus (PC), bilateral temporal poles (TP) and left temporoparietal junction (TPJ). On the other hand, nonverbal cues elicited activation in the putative "mirror neuron system" associated with action observation as well as the bilateral amygdala, right STS and right FFG related to perception of salient social stimuli. However, direct comparisons between the processing of verbal and nonverbal information by using fMRI are not suitable for drawing conclusions on areas specifically involved in social cognitive processes of interest because of differences in basic sensory and cognitive processing between domains (e.g., language-associate areas for verbal and motion-associated areas for dynamic nonverbal stimuli).

Efforts to identify neural regions that track the intensity of evaluative interpersonal judgments revealed the specific involvement of the posterior cingulate cortex (PCC) and the amygdala (Schiller et al., 2009). However, it is not clear to what extent these areas tend to be more strongly involved dependent on whether the evaluation based on verbal or on nonverbal information because both domains were used simultaneously in the referred study.

5.1.4 Impression formation in individuals with high-functioning autism

The core diagnostic criteria of the pervasive developmental disorder autism include impaired development of and qualitative deficits in social communication and reciprocal social interaction (10th revision of the International Classification of Diseases, ICD-10, World Health Organization). These impairments have been explained by reduced salience of social stimuli and specific deficiency in theory of mind (Frith, 2001, 2003; Klin et al., 2003). Particularly in normative-IQ individuals with autism, i.e., HFA, there is a discrepancy between their preserved or even superior logical, rule-based reasoning skills and their social cognitive impairments. While they are able to solve even social cognitive problems when all elements are presented explicitly and verbally in an experimental setting, they do not show correspondent adaptive social behavior in more naturalistic, everyday life situations (Klin et al., 2003). In latter, they have to apply mentalizing spontaneously and to integrate multiple and incomplete information in order to meet the demands of moment-to-moment social encounters.

Little is known about how individuals with HFA are performing when they have to form impressions about other people. However, in order to form an impression, one needs to be capable of decoding relevant person information provided by, for instance, verbal action descriptions or expressive nonverbal cues, and to make conclusions about intentions and other mental states explaining the perceived behavior. While individuals with HFA were shown to be able to infer personality traits from verbal action descriptions (Ramachandran, Mitchell, & Ropar, 2009), they seem to have more robust difficulties with the decoding of nonverbally transmitted social information (Ashwin, Chapman, Colle, & Baron-Cohen, 2006; S. Baron-Cohen et al., 1999; Critchley et al., 2000; Schultz et al., 2000; Senju, Southgate, White, & Frith, 2009). Furthermore, in more complex settings, where multiple pieces of information are given, these data have to be integrated in a general evaluation. It is an open question, which of these cognitive computational components individuals with HFA can realize and how they differ from the neurotypical processing.

5.2 Experimental design and hypotheses

Studies 2 and **3** (Kuzmanovic et al., 2012; Kuzmanovic, Schilbach, Lehnhardt, Bente, & Vogeley, 2011) focused on impression formation based on verbal and nonverbal person information. **Study 2** implemented two types of behavioral tasks, a basic and a complex one, and examined the impression formation in individuals with HFA and matched controls (both N = 15). In the *basic task* (see Fig. 5.1C), participants were instructed to evaluate target persons on a 6-point rating scale (ranging from very negative to very positive) based on one single piece of information: either verbal (V) or nonverbal (N). Verbal information consisted of one-sentence action description (12 positive, +, and 12 negative, –, see Fig. 5.1B), and was introduced as a statement by a friend of the target person in reference to her prior work place. Short video clips displaying expressive nonverbal cues (such as direct gaze or smile; 12 positive and 12 negative; see Fig. 5.1A) were used as nonverbal information, which were said to be a 'thin slice' of the face-to-face job interview overlayed onto a virtual character. Before evaluating single stimuli, participants in **Study 2** underwent the *complex task*, in which they formed their impressions always based on a pair of stimuli: one verbal and one nonverbal. These pairs were either *congruent* (both stimuli were positive or negative) or *incongruent* (one stimulus was positive and one negative).

Study 3 used the basic task to investigate the neural correlates of first impressions by using fMRI, thereby comparing the evaluations based on verbal and nonverbal information (see Fig. 5.1). Because a direct comparison between verbal and nonverbal information processing would be unspecific due to additional differences in basic sensory and cognitive processing between domains (see 1.4.3), we identified neural regions where the activity correlated with increasing 'strength of evaluation' (SoE), separately for verbal and nonverbal stimuli. We supposed that neural regions where the activity systematically increases with increasing SoE should have a central role in the generation of interpersonal impressions. In order to induce a sufficient variance of SoE, we included neutral verbal and nonverbal stimuli, so that SoE could vary from 0 (neutral middle on a 7-point rating scale) to 3 (absolute distance from 0 on a 7-point rating scale, including both very positive and very negative ratings).

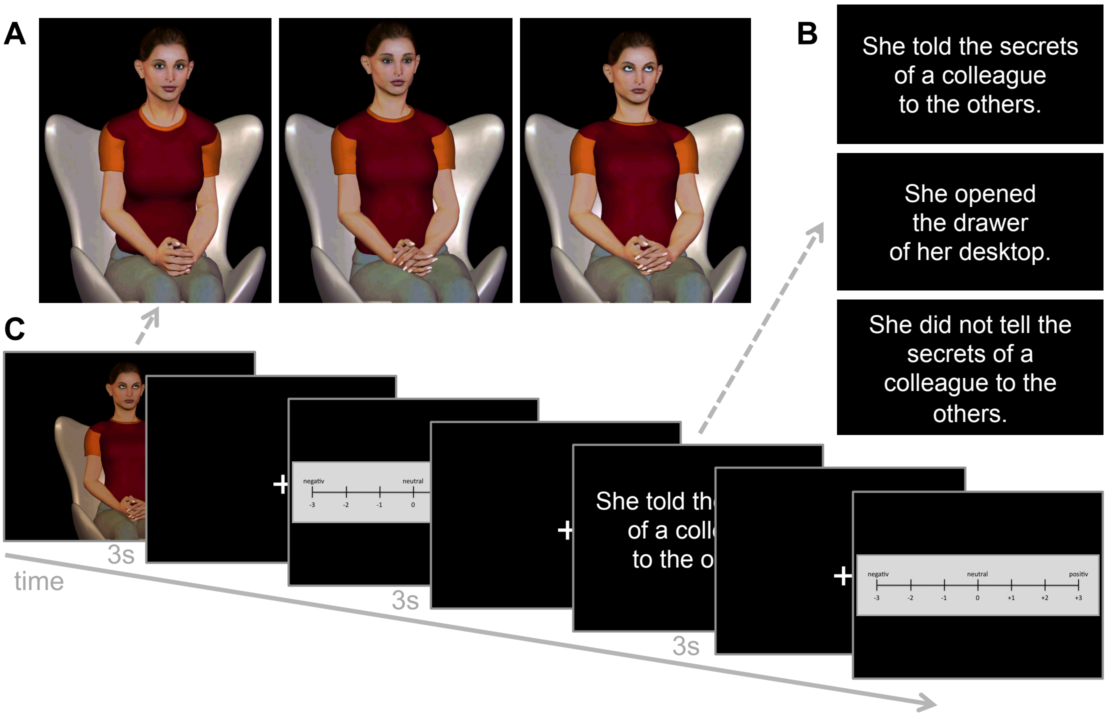

Fig. 5.1. Examples of verbal and nonverbal stimuli and experimental procedure of the basic impression formation task from **Study 3**. **A)** Example frames from positive, neutral and negative nonverbal video stimuli; **B)** example sentences of positive, neutral and negative verbal stimuli; and **C)** an example of two subsequent experimental trials: verbal and nonverbal stimuli were presented in a randomized order and rated by participants on a 7-point global evaluation rating scale. In **Study 2** only positive and negative stimuli were used and the rating scale had 6 points, without the neutral mid-point.

For the **Study 2** we hypothesized that individuals with HFA would have difficulties in decoding and consideration of nonverbal cues rather than verbal information during impression formation, particularly during the *complex incongruent task* in which conflicting information had to be integrated. We tested for group differences (between-subject factor group, i.e., HFA vs. control, included in all analyses) in an mixed ANOVA for the *basic task* (within-subject factors: domain, i.e. verbal vs. nonverbal, and valence, i.e., positive vs. negative) and in two mixed ANOVAS for the *complex task* (*congruent* trials: within-subject factor valence, i.e., positive vs. negative; *incongruent* trials: within-subject factor valence combination, i.e., V+N– vs. V–N+). Additionally, we computed *relative impacts* of verbal and nonverbal stimuli within the *complex incongruent task* based on subjective ratings of the single stimuli in the *basic task*, therefore controlling for inter-individual differences in the evaluation of person information (see Kuzmanovic et al., 2011; within-subject factors: domain, i.e. verbal vs. nonverbal, and valence, i.e., positive vs. negative).

In **Study 3** we explored putative differences in neural correlates of verbal and nonverbal social information that evoke increasing strengths of evaluative person judgment. We tested whether the neural regions specifically involved in interpersonal evaluation, i.e. amygdala and PCC (Schiller et al., 2009), can be functionally dissociated with respect to the domain of information.

5.3 Findings and conclusions

5.3.1 Impression formation in high-functioning autism

The *basic task* in **Study 2** did not reveal any differences between HFA and controls (see Fig. 5.2A; results are reported as significant at $p < .05$; for exact inferential statistics see Kuzmanovic et al., 2011, Table 2). There were no significant main effects of group or domain, indicating that in general the ratings of single stimuli did not differ between HFA and controls or between the verbal and nonverbal domain. However, there was a significant interaction between valence and domain indicating that verbal stimuli were evaluated more extremely than nonverbal stimuli. Thus, this highlights the importance of putting the relative impact of verbal and nonverbal information within incongruent integrative decisions into perspective with their basic ratings. Furthermore, there was a significant main effect of valence confirming the different valence of positive and negative stimuli. No other interactions reached significance (group x domain, group x valence, or group x domain x valence).

The *complex task* in **Study 2** revealed domain dependent group differences only for the incongruent but not for congruent trials (see Fig. 5.2B). In the *complex congruent task* there was a significant main effect of valence indicating that positive and negative pairs of stimuli were rated differently, but there was no significant main effect of group or interaction between group and valence. In the *complex incongruent task*, there was a significant main effect of valence combination showing that in general V–N+ trials were rated more negatively than V+N– trials indicating a more robust influence of the verbal domain, but there was no significant main effect of group. However, there was a significant interaction between group and valence combination. Thus, although both groups took the verbal information more strongly into account, this effect was more pronounced in the HFA group.

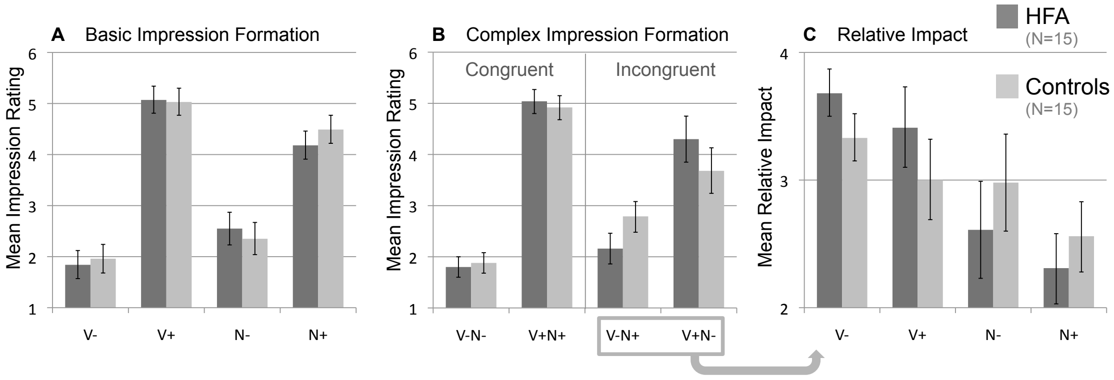

Fig. 5.2. Results from **Study 2** relating to impression formation ratings by HFA and control participants based on verbal and nonverbal information. **A)** Mean ratings for the *basic task* based on single pieces of information; **B)** mean ratings for the *complex task* based on a combination of verbal and nonverbal information separated for *congruent* and *incongruent* trials; and **C)** mean *relative impact* of verbal and nonverbal information within *complex incongruent* trials. Error bars show 95% C.I.

By relying on individual ratings of the correspondent stimuli from each incongruent pair, the *relative impact* provided a more precise measure of the influence of the verbal and nonverbal domain in **Study 2**. Again, there was a significant main effect of domain, which confirms that in general, verbal information had a greater impact on impression formation than nonverbal information (see Fig. 5.2C). Importantly, this effect again differed between the groups, as there was a significant interaction between group and domain. Pair-wise comparisons revealed that HFA participants relied more strongly on verbal information than control participants. Furthermore, there was a significant main effect of valence demonstrating a greater impact of negative as compared to positive information, but no significant main effect of group or interaction effects between the factors valence and domain, group and valence, or group, domain and valence.

Taken together, these results show that individuals with HFA are well able to evaluate persons based on both verbal and nonverbal information, but only in a very simplified setting where all stimuli are presented separately and independently from each other. By contrast, in a more complex setting, where multiple pieces of conflicting information have to be integrated into a global judgment, individuals with HFA tend to neglect nonverbal cues and to rely preferentially on verbal information. This points toward a compensational rule-based dealing with mentalistic contents. Such cognitive style may allow for the deductive extraction of constructs or abstract meanings of social stimuli, which is easier when the more explicitly coded verbal information is presented. However, when subtle nonverbal cues have to exert influence within a multifaceted evaluation, spontaneous affective and cognitive reactions may be more important (Senju et al., 2009), which are shown to be reduced in face of nonverbal stimuli in HFA (Schwartz, Bente, Gawronski, Schilbach, & Vogeley, 2010).

Critically, these conclusions are rather indirect because they rest upon the differential characteristics of verbal and nonverbal information and thus may profit from the more direct approach of revealing underlying neural mechanisms of impression formation based on different domains by using fMRI (see **Study 3**, 5.3.2). Nonetheless, the results clearly support “a dissociation between *knowing* what a cue means on the one hand, and, on the other hand, *acting* upon it based on motivational predispositions to respond to salient social stimuli” (Kuzmanovic et al., 2011, p. 611).

5.3.2 Neural correlates of impression formation

The results from **Study 3** revealed distinct neural correlates of increasing strength of subjective impressions based on verbal and nonverbal stimuli, respectively. While generally confirming that amygdala and PCC are specifically involved in interpersonal evaluation (Schiller et al., 2009), we demonstrated that the amygdala was recruited for dynamic nonverbal, and the PC at the border to PCC (PC/PCC) for verbal stimuli of increasing impact (see Fig. 5.3; significance threshold for fMRI group results: $p_{FWE\text{-}corr} < .05$). These effects were shown to be independent of the arousal and the valence of stimuli (see Kuzmanovic et al., 2012), thus emphasizing their relation to the increasing intensity of judgments.

This neurofunctional dissociation indicates qualitatively different cognitive processes underlying impression formation dependent upon the domain of information: while nonverbal stimuli seem to provoke more strongly affective, salience-dependent processing consistently linked to the amygdala (Sander, Grafman, & Zalla, 2003; Sergerie, Chochol, & Armony, 2008; Zald, 2003), verbal stimuli may be stronger tied to social inferential processing associated with the PC/PCC (Lieberman, 2010). The stronger link of the amygdala to nonverbal social cues is in good accordance with studies that consistently demonstrated its central role in judging faces with regard to valence or trustworthiness (Gerber et al., 2008; Rule et al., 2011; Said, Baron, & Todorov, 2009; Todorov, 2008; Todorov & Engell, 2008; Winston, Strange, O'Doherty, & Dolan, 2002). On the other hand, the systematic recruitment of the PC/PCC by increasingly influential verbal stimuli fits well with previous studies showing its involvement in processing of emotionally salient and valent words (Maddock, Garrett, & Buonocore, 2003; Posner et al., 2009).

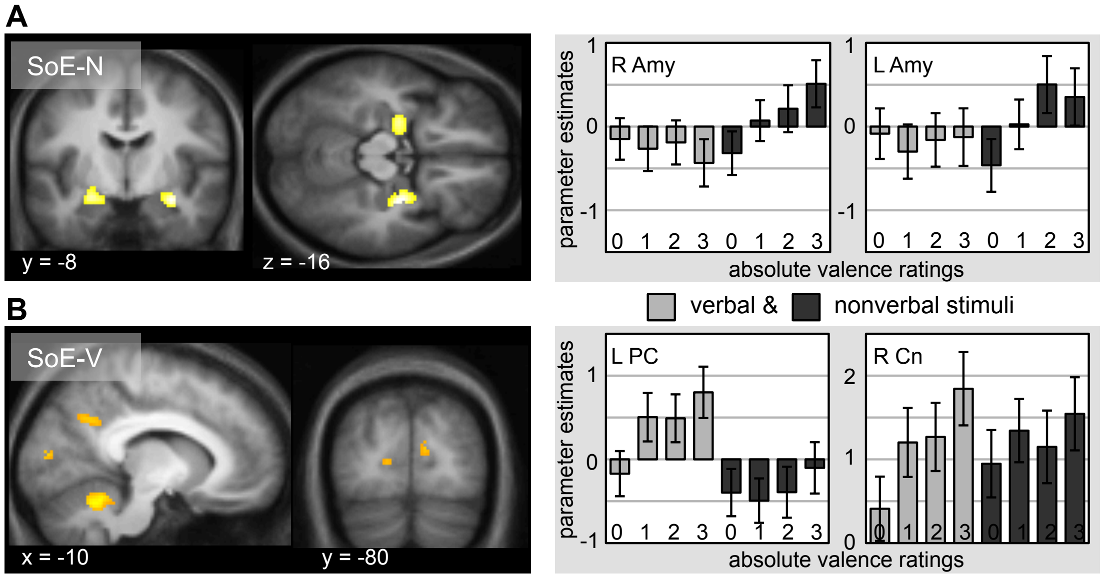

Fig. 5.3. Results from **Study 3** showing brain regions responsive to the outcome of subjective evaluative impressions based on verbal or nonverbal person information. **A)** When processing nonverbal stimuli (N), the activity in the bilateral amygdala correlated with the increasing absolute valence ratings as a measure of the strength of evaluation (SoE); **B)** whereas for verbal stimuli (V) this effect occurred in the precuneus at the border to posterior cingulate cortex, in the cuneus and the cerebellum. Plots are derived by a supplementary analysis modeling events with different absolute ratings (0, 1, 2 or 3) as separate regressors. L, left; R, right; Amy, amygdala; PC, precuneus, Cn, cuneus; error bars show 90% C.I..

With regard to the results of **Study 2**, the finding that impression formation based on nonverbal stimuli is mediated by the bilateral amygdala associated with affective processing of salient social stimuli supports the conclusions made in 5.3.1 concerning the reduced spontaneous affective responses to nonverbal social cues in HFA.

6 Studies 4 and 5: Different looks on animacy – mind attribution in high-functioning autism

6.1 Theoretical background

6.1.1 The relevance of animacy perception for social cognition

Animacy, defined as the interpretation or experience of other entities as intentional, mindful agents, is an important basis for all social cognitive processes that involve inferences about mental states of others (Santos, David, Bente, & Vogeley, 2008). From the philosophical viewpoint there actually should be an “other minds problem”: because we never have direct access to minds of others but only to our own mental states, we actually never can confidently conclude that others should have minds at all (Epley & Waytz, 2010). However, this problem does not occur in everyday life, as we are extraordinarily able to think about other minds and tend to attribute humanlike mental states not only to other persons, but also to animals, and even to computers or natural events. This huge time amount spent on thinking about invisible minds can be justified by its contribution to explaining, understanding and predicting the otherwise random behavior of others (Dennett, 1987). Thus, the perception of animacy as a first step in mind inference is an important building block of social cognition.

A very elegant demonstration of animacy perception has been conducted by Heider and Simmel (1944) by using short videos with dynamically moving geometric shapes. Although triangles have nothing in common with mindfulness, their interactive movement pattern induced an impression of animacy and an interpretation of events in terms of mental states. This fundamental work inspired many into using such paradigms in order to investigate mind attribution in healthy as well as in autistic samples.

6.1.2 Neural correlates of animacy perception

Using interactively moving geometric shapes to evoke animacy impressions, neuroimaging studies have revealed the recruitment of brain regions related to different aspects of social cognition, thus confirming the initiating function of animacy for social cognition. These brain regions include the STS, the superior temporal gyrus (STG) and the FFG 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 judgments (Castelli, Happe, Frith, & Frith, 2000; Gobbini, Koralek, Bryan, Montgomery, & Haxby, 2007; Lieberman, 2010; Santos et al., 2010; Schultz et al., 2003; Tavares, Lawrence, & Barnard, 2008; Wheatley, Milleville, & Martin, 2007). Thus, animacy appears to be effective in triggering comprehensive social processing and can be used to explore the ability to attribute mind to animated agents.

6.1.3 Animacy perception in individuals with high-functioning autism

As described before (see 5.1.4), individuals with HFA show specific cognitive deficits relating to the representation of mental states of others, which has been denoted as “mindblindness” (Simon Baron-Cohen, 1995). Especially the spontaneous, intuitive attribution of and reaction upon mental states seems to be robustly impaired, while analytic reasoning may enable HFA individuals to perform well on explicit ToM-tasks in simplified experimental settings (Klin, 2000; Senju et al., 2009).

Implying mind attribution, animacy perception in dynamic geometric shapes was one of the paradigms, which were sensitive enough to detect these subtle characteristics of altered social processing in HFA. Individuals with HFA were specifically impaired in social but not in physical attribution (Klin & Jones, 2006), and interpreted animated stimuli less frequently in terms of social and mentalistic aspects (Klin, 2000). Furthermore, neuroimaging studies revealed reduced activity in important nodes of the social neural network including STS, TPJ, dmPFC, amygdala, TP and FFG (Castelli, Frith, Happe, & Frith, 2002; Spengler, Bird, & Brass, 2010).

6.2 Experimental design and hypotheses

Study 4 (Santos et al., 2010) aimed to investigate neural correlates of a parametric increase of experience of animacy. Thus, in order to create a more sensitive measure for disturbances of the mind attribution ability, animacy perception was induced in varying degrees along a continuum rather than as a dichotomy. This was achieved by a systematic modulation of movement characteristics of geometric shapes that are dependent on the degree of interaction between objects. Following motion parameters have been shown to provoke increased impression of animacy by ascribing the cause of the motion to the observed geometric shape (Santos et al., 2008): directionality (direction of the motion and changes in direction), discontinuity (pauses in the trajectory, only in the presence of an second object) and responsiveness (reaction of some part of the environment to object's movement).

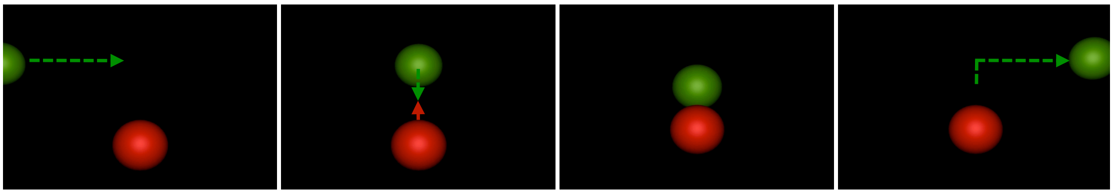

Fig. 6.1. Four frames extracted out of an example stimulus video from **Studies 4** and **5** containing "approach" and "responsiveness" with arrows illustrating the pathways of movements. Across all stimuli, the beginning and the end were exactly the same showing a red sphere in the front and a green sphere entering and exiting the scene. The middle part was systematically varied across the four stimulus categories. In the least animated category, there was no additional action, i.e., the green sphere passed by without a stop or a change in the direction and the green sphere showed no reaction (category 1, no approach/ no responsiveness). In the most animated category, the green sphere stopped in front of the red one (frame 2) and approached it while the red sphere responded by moving towards the green sphere (frame 3; category 4, approach/ responsiveness).

Consequently, stimulus videos were created, in which these critical motion parameters were systematically modulated. All stimulus videos had the same basic scenery including two spheres, a green one in the background crossing the scene horizontally and a red one in the front. Discontinuity and directionality were used to create an impression of "approach" (see Fig. 6.1). Here, the green sphere interrupted its movement and changed its direction towards the red sphere. Furthermore, the impression of "responsiveness" was induced by the movement of the red sphere towards the green sphere. The full combination of factors approach and responsiveness resulted in four categories of stimuli with increasingly animated movement patterns: 1) no approach/ no responsiveness; 2) no approach/ responsiveness; 3) approach/ no responsiveness; and 4) approach/ responsiveness (Santos et al., 2008). While being in the scanner, 15 male healthy participants rated in total 104 stimuli on a four-point scale ranging from "physical" to "person-like". We hypothesized that neural regions previously identified to be involved in animacy perception (see 6.1.2) would increase their activity parametrically with increasing animacy. Furthermore, we compared the neural tracking of increasing animacy based i) on an *objective* measure of varying animacy, i.e. movement features (*objective animacy*); and ii) on a *subjective* measure of varying animacy, i.e. subjective ratings (*subjective animacy*) and expected overlapping effects of these two measures.

After examining neural correlates of increasing animacy in healthy participants, **Study 5** focused on the comparison between adults with HFA and matched controls (both N = 13) (Kuzmanovic et al., under review). In particular, by using a more sensitive measure for deficits in mind attribution, the study aimed to provide empirical confirmation of the assumption that individuals with HFA apply different cognitive strategies when processing social information. More specifically, because HFA show preserved skills for physical attributions (Klin & Jones, 2006), the applied cognitive strategies might rely more on feature-based processing, i.e., focusing on physical properties of stimuli, thereby resulting in differential emotional and/or cognitive responses and hence altered subjective experience (Kuzmanovic et al., 2011; Piggot et al., 2004). Thus, we contrasted the two groups with regard to increasing *objective* and *subjective animacy*. We hypothesized that HFA and controls would differ with regard to the subjective animacy experience, but not with regard to the feature-based processing of the stimuli. Furthermore we computed the correlation between subjective and objective measures of animacy for each participant, referred to as the subjective-objective fit (SOF). Indicating the propensity to recognize animacy-relevant movement patterns, the SOF was used to compare the HFA and the control group with respect to interindividual differences in animacy recognition and their neural correlates.

6.3 Findings and conclusions

6.3.1 Increasing animacy in healthy individuals

In **Study 4**, on the behavioral level, the analysis of variance confirmed that the factors approach ($F(1,14) = 82.14$, $p < .001$, $r = .92$) and responsiveness ($F(1,14) = 10.92$, $p < .05$, $r = .66$), but no other movement or scenery features, had an effect on the animacy ratings. On the neural level, the increasing *subjective animacy* was correlated with the activity in the bilateral insula, the STS and STG, the mOFC extending into the pre- and subcallosal ACC, and left FFG (see Santos et al., 2010; significance threshold: $p_c < .05$ at the cluster-level, corrected for multiple comparisons and $p < .005$ at the voxel-level, uncorrected).

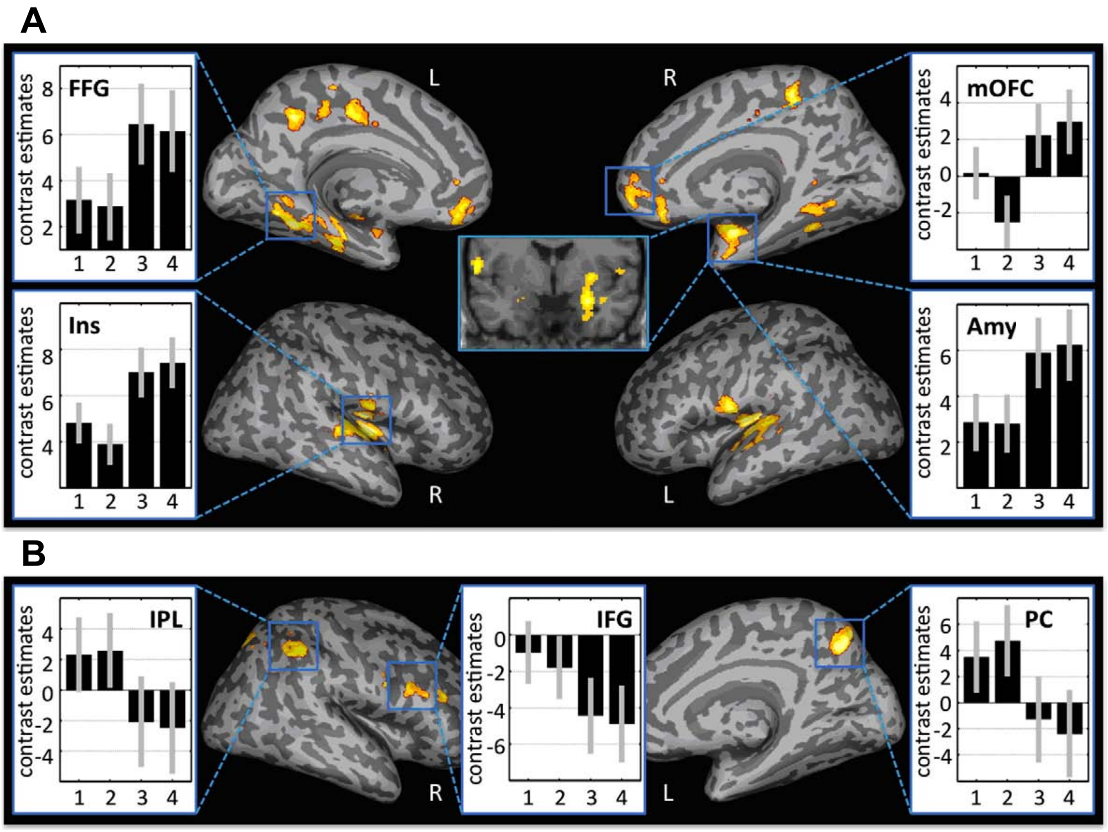

Fig. 6.2. Results from **Study 4** showing neural regions responsive to increasing and decreasing *objective animacy* as defined by movement patterns of the stimuli. **A)** Neural regions where the activity correlated with the increasing objective animacy including the insula, the amygdala, the superior temporal gyri, the FFG and the medial prefrontal cortex; and **B)** the opposite effect of decreasing objective animacy yielding regions in bilateral inferior frontal and parietal cortices as well as in the superior precuneus (see Santos et al., 2010). Plots illustrate corresponding contrast estimates obtained for movies with varying movement patterns (1, no approach/ no responsiveness, 4, approach/ responsiveness). L, left; R, right; mOFC, medial orbitofrontal cortex; Amy, amygdala; FFG, fusiform gyrus; Ins, insula; IPL, inferior parietal lobule; IFG, inferior frontal gyrus; PC, precuneus; error bars show 90% C.I..

An overlapping but more extended network was correlated with increasing *objective animacy* (see Fig. 6.2) including the bilateral insula extending into the right amygdala, the bilateral STG, the right TP, the ACC and the mOFC, and the bilateral FFG (significance threshold: $p_c < .05$ at the cluster-level, corrected for multiple comparisons and $p < .0005$ at the voxel-level, uncorrected; for the full list of results see Santos et al., 2010). In contrast to the effect of decreasing animacy indicating the engagement of frontoparietal brain regions associated with attention and action observation (see Fig. 6.2 and Santos et al., 2010), this aggregate of brain regions is part of the social neural network and reflects social perceptual and evaluative processes (Lieberman, 2010). Thus, we confirmed that the experience of animacy depending on mind-implying movement properties is able to gradually engage social processing, irrespective of whether the stimuli had an anthropomorphic appearance (Wheatley et al., 2007).

6.3.2 Decoding strategies for animacy in high-functioning autism

Study 5 replicated the increasing recruitment of social neural regions for both increasing *subjective* and *objective animacy* in healthy participants, including bilaterally the insula, the amygdala, the STG, the TP (for objective animacy only right TP), the FFG (for subjective animacy only left FFG) and the ventral and dorsal mPFC (for the full list of results see Kuzmanovic et al., under review; significance threshold for fMRI group results: $p_c < .05$ at the cluster-level, corrected for multiple comparisons and $p < .001$ at the voxel-level, uncorrected). However, the focus of this study was to compare HFA and controls, which revealed specific differences and similarities dependent on the measure of animacy. On the behavioral level, there was neither a significant group difference in ratings of the four stimulus categories with regard to “person-likeness” (see Fig. 6.3C) nor in the SOF scores, indicating comparable overt performances between the groups in the experimental task. Similarly, on the neural level, the increasing *objective animacy* did not reveal any significant group differences but a common network shared by both groups including 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 et al., 2007), the vmPFC plays an important role in generating integrative, evaluative judgments (Phan et al., 2004; Zysset, Huber, Samson, Ferstl, & von Cramon, 2003). Together, these comparable outcomes indicate that both groups were able to recognize the objective features of the stimuli, and that the common neural substrate of this performance seems to be related to perceptual analysis and its evaluation.

In contrast, when regarding the *subjective animacy,* there was a significant group difference showing that the bilateral activity in insula, STG, TP, amygdala and dmPFC was correlated more strongly with increasing subjective animacy in controls than in HFA (see Fig. 6.3A). Furthermore, the correlation between the general activity in the left STS, right TPJ and the left superior frontal gyrus, and the SOF scores was significantly stronger for the control than the HFA sample (see Fig. 6.3B).

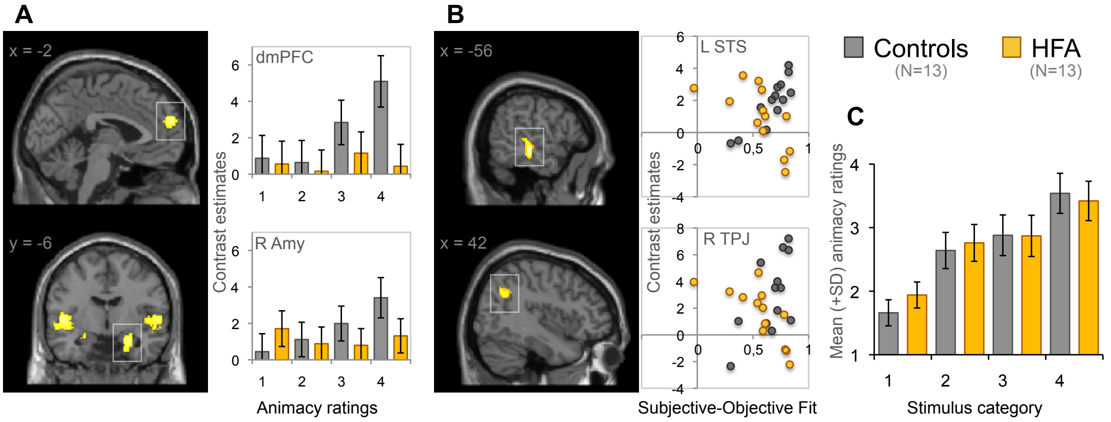

Fig. 6.3. Neuroimaging and behavioral results from **Study 5**. **A)** Brain regions where the correlation between the increasing *subjective animacy* (as indexed by participants' ratings) and activity was significantly greater in controls than in HFA including bilaterally the dmPFC, the amygdala, the insula and the temporal cortices. The plots were derived from a supplementary 4 x 2 categorical model including regressors for each response option, separately for the two groups. **B)** Brain regions where the activity correlated with the subjective-objective fit (SOF, the fit between the ratings of a participant and the movement patterns of stimuli) to a significantly greater extent in the control than in the HFA group including the STS, the TPJ and the superior frontal gyrus. For illustrative purposes, scatter charts showing the relation between the SOF and the contrast estimates of the significantly correlated neural regions are depicted. **C)** Ratings of the "person-likeness" separated for different stimulus categories (see 6.2 and Fig. 6.1). L, left; R, right; dmPFC, dorsomedial prefrontal cortex; Amy, Amygdala; STS, superior temporal sulcus; TPJ, angular gyrus corresponding to the temporoparietal junction; error bars show 90% C.I..

Taken together, these results indicate dissociable cognitive strategies applied during the task, that for the HFA group do not incorporate neural regions implicated in mental inference (Amodio & Frith, 2006; Castelli et al., 2002; Schultz et al., 2003; Tavares et al., 2008; Van Overwalle & Baetens, 2009; Wheatley et al., 2007) and salience-dependent affective processing (Martin & Weisberg, 2003; Pessoa, 2008; Robinson, Laird, Glahn, Lovallo, & Fox, 2010; Santos et al., 2010) as a result of reduced modulation of subjective experience by increasingly social stimuli. Thus, we provided 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. Paralleling the findings from **Study 2**, neurofunctionally underpinned by the Study 3, these results support 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 (Klin et al., 2003).

7 General discussion

The presented studies used nonverbal and animated behavior to induce discrete social cognitive processes in order to make them accessible for fundamental as well as for comparative-clinical investigations. In general, the construction of a subjective meaning of nonverbal behavior appears to be heavily influenced by the intrinsic predispositions to ascribe salience and significance to these stimuli thereby modulating further experiences and judgments (Ambady & Weisbuch, 2010; Klin et al., 2003).

More specifically, in **Study 1** the increasing duration of the direct gaze of a social other systematically increased ratings of likeability and the activity of the mPFC associated with complex social cognitive computations such as mentalizing and conflict and outcome monitoring. Hence, our results support the proposed link between direct gaze and understanding self-relevant intentions of others. This link can be deduced from the enhanced but ambiguous communicational content of a prolonged stare, which can convey social interest but also demonstration of dominance and thus requires continuous decoding for the sake of an adaptive social behavior. Overcoming the traditional restriction to *gaze direction*, our findings thus indicate that the systematic investigation of dynamic and subtle nonverbal parameters such as *gaze duration* may help to better characterize the link between direct gaze and complex social cognitive processes.

Furthermore, **Studies 2** and **3** explored putative differences in the quality and relative influence of the processing of verbal and nonverbal person information in the context of impression formation. While increasing strength of interpersonal evaluation based on nonverbal stimuli was associated with the activity in the bilateral amygdala, verbal stimuli differentially recruited the PC/PCC, the cuneus and the cerebellum. Thus, **Study 3** provided evidence for qualitatively different processing paths dependent on the domain of information. Not only does the amygdala play a central role in affective and salience-dependent processing (Sergerie et al., 2008), this region has also been implicated in automatic and implicit processing, for example when emotional facial expression have been presented subliminally (Liddell et al., 2005; Whalen et al., 2004; Whalen et al., 1998) or when there was no explicit instruction to appraise facial stimuli (Engell, Haxby, & Todorov, 2007; Phelps et al., 2000; Todorov & Engell, 2008; Winston et al., 2002). Thus, the amygdala may be a part of a network that mediates automatic responses to meaningful social cues such as gaze following, which cannot be suppressed (Driver et al., 1999) without reaction time costs (Schilbach, Eickhoff, Cieslik, Kuzmanovic, & Vogeley, 2011), or the ability of cortically blind persons to detect facial expressions above the chance level (de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999; Pegna, Khateb, Lazeyras, & Seghier, 2005). By contrast, the PC/PCC associated with increasing strength of evaluation based on verbal information has been assigned to brain regions involved in explicit and reflective social cognition (Lieberman, 2010), highlighting the relatively stronger link between verbal stimuli and deliberate processing (Evans, 2008; Lieberman, 2007).

The importance of spontaneous and affective responses to nonverbal social cues becomes even more apparent when considering their role in psychiatric disorders. For example, the amygdala response to subliminally presented fearful facial expressions is exaggerated in patients with posttraumatic stress disorder characterized by hyperarousal and disinhibited trauma re-experiencing indicating an impaired gating of affective sensory input (Rauch et al., 2000). By contrast, in HFA, nonverbal cues induce an attenuated neural response in amygdala as compared to controls (Ashwin, Baron-Cohen, Wheelwright, O'Riordan, & Bullmore, 2007; S. Baron-Cohen et al., 1999), have diminished influence on reports about feelings (Schwartz et al., 2010) and elicit reduced spontaneous responses (Senju et al., 2009), although this has not directly been demonstrated with subliminally presented stimuli. In the same line, the findings of **Study 2** support the idea of reduced spontaneous affective responses to nonverbal social information in HFA by revealing its diminished impact within multimodal impression formation, although isolated stimuli were recognized equally well by both HFA and control participants. In addition, the assumption that influences of nonverbal cues on social judgments are mediated by affective responses is further underpinned by the specific recruitment of the amygdala for increasingly extreme person evaluations based on nonverbal information in **Study 3**.

Finally, **Studies 4** and **5** demonstrated that the activity in an extended social neural network was correlated with objectively and subjectively measured increase of animacy in dynamic geometric figures in control participants. Moreover, **Study 5** showed that in contrast to controls, the increasing *subjective* experience of animacy in individuals with HFA was not tracked by the activity of the amygdala, the dmPFC, the insula, the STG and the TP. This finding support the proposed altered cognitive style in HFA, which might rely more strongly on feature-based attributions, as confirmed by the comparable recognition of animacy and by common neural correlates of *objective* animacy based on stimulus features across HFA and control participants. Thus, in good accordance with **Study 3**, **Study 5** provides empirical evidence for the assumption of reduced spontaneous affective and inferential responses in HFA along with a stronger preference for deductive feature-based reasoning during the decoding of social stimuli (Klin & Jones, 2006; Klin et al., 2003).

In contrast to physical environments where consequences and causes are clearly definable, social environments are characterized by a great uncertainty because actions are originated from people and depend on their intentions and spontaneous reactions. Consequently, a fast working mechanism is needed to detect and infer covert mental states of others indicated by a variety of cues including nonverbal behavior as well as verbal communication in order to enable dynamic regulation of one’s own actions and reactions. Thereby, nonverbal social information has a primacy status with regard to cognitive processing by relying on phylogenetically older mechanisms that are effective from the early childhood on and are high in automaticity (Ambady & Weisbuch, 2010). The present work provides empirical evidence for this notion by demonstrating specific influences of the nonverbal information on interpersonal judgment outcomes via the amygdala and by showing that nonverbal cues trigger extended neural responses related to complex perceptual, affective and evaluative analyses. Furthermore, by identifying attenuation in exactly these responses to nonverbal stimuli in HFA, the present findings promote the importance of spontaneous cognitive and affective processes in adaptive social functioning and contribute to the better characterization of this disorder. Finally, the relatively closer link between nonverbal behavior and automatic and affective processes has important implications for social decisions made in private and public domains, that are moreover often embedded in modern media with increasing availability of pictorial information (Frey, 1999).

8 References

Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: role of the STS region. *Trends Cogn Sci, 4*(7), 267-278.

Ambady, N., & Weisbuch, M. (2010). Nonverbal Behavior. In S. T. Fiske, D. T. Gilbert & G. Lindzey (Eds.), *Handbook of Social Psychology*. New York: McGraw Hill.

Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: the medial frontal cortex and social cognition. *Nat Rev Neurosci, 7*(4), 268-277.

Argyle, M., & Cook, M. (1976). *Gaze and mutual gaze*. Cambridge: Cambridge University Press.

Argyle, M., Lefebvre, L., & Cook, M. (1974). The meaning of five patterns of gaze. *Eur. J. soc. Psychol., 4*(2), 125-136.

Ashwin, C., Baron-Cohen, S., Wheelwright, S., O'Riordan, M., & Bullmore, E. T. (2007). Differential activation of the amygdala and the 'social brain' during fearful face-processing in Asperger Syndrome. *Neuropsychologia, 45*(1), 2-14.

Ashwin, C., Chapman, E., Colle, L., & Baron-Cohen, S. (2006). Impaired recognition of negative basic emotions in autism: a test of the amygdala theory. *Soc Neurosci, 1*(3-4), 349-363.

Baron-Cohen, S. (1995). *Mindblindness : an essay on autism and theory of mind*. Cambridge, Mass. ; London: MIT Press.

Baron-Cohen, S., Ring, H. A., Wheelwright, S., Bullmore, E. T., Brammer, M. J., Simmons, A., et al. (1999). Social intelligence in the normal and autistic brain: an fMRI study. *European Journal of Neuroscience, 11*(6), 1891-1898.

Bente, G., & Kraemer, N. C. (2008). Effects of nonverbal communication. In W. Donsbach (Ed.), *International encyclopedia of communication* (pp. 3334-3339). London: Blackwell Publishing.

Bente, G., Petersen, A., Kraemer, N. C., & de Ruiter, J. P. (2001). Transcript-based computer animation of movement: evaluating a new tool for nonverbal behavior research. *Behavior Research Methods, Instruments, & Computers, 33*(3), 303-310.

Bente, G., Senokozlieva, M., Pennig, S., Al-Issa, A., & Fischer, O. (2008). Deciphering the secret code: a new methodology for the cross-cultural analysis of nonverbal behavior. *Behavior Research Methods, 40*(1), 269-277.

Brooks, C. I., Church, M., A., & Fraser, L. (1986). Effects of duration of eye contact on judgments of personality characteristics. *Journal of Social PSychology, 126*, 71-78.

Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends Cogn Sci, 4*(6), 215-222.

Castelli, F., Frith, C., Happe, F., & Frith, U. (2002). Autism, Asperger syndrome and brain mechanisms for the attribution of mental states to animated shapes. *Brain, 125*(Pt 8), 1839-1849.

Castelli, F., Happe, F., Frith, U., & Frith, C. (2000). Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. *Neuroimage, 12*(3), 314-325.

Choi, V. S., Gray, H. M., & Ambady, N. (2005). The glimpsed world: Inintended communication and unintended perception. In R. R. Hassin, J. S. Uleman & J. A. Bargh (Eds.), *The new unconcsious* (pp. 309-333). New York: Oxford University Press.

Critchley, H. D., Daly, E. M., Bullmore, E. T., Williams, S. C., Van Amelsvoort, T., Robertson, D. M., et al. (2000). The functional neuroanatomy of social behaviour: changes in cerebral blood flow when people with autistic disorder process facial expressions. *Brain, 123 (Pt 11)*, 2203-2212.

de Gelder, B., Vroomen, J., Pourtois, G., & Weiskrantz, L. (1999). Non-conscious recognition of affect in the absence of striate cortex. *Neuroreport, 10*(18), 3759-3763.

Delgado, M. R., Frank, R. H., & Phelps, E. A. (2005). Perceptions of moral character modulate the neural systems of reward during the trust game. *Nat Neurosci, 8*(11), 1611-1618.

Dennett, D. C. (1987). *The intentional stance*. Cambridge, MA: MIT Press.

Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E., & Baron-Cohen, S. (1999). Gaze perception triggers reflexive visuospatial orienting. *Visual Cognition, 6*, 509-540.

Droney, J. M., & Brooks, C. I. (1993). Attributions of self-esteem as a function of duration of eye contact. *J Soc Psychol, 133*(5), 715-722.

Dunbar, R. I., & Shultz, S. (2007). Evolution in the social brain. *Science, 317*(5843), 1344-1347.

Einav, S., & Hood, B. M. (2006). Children's use of the temporal dimension of gaze for inferring preference. *Developmental Psychology, 42*, 142-152.

Engell, A. D., Haxby, J. V., & Todorov, A. (2007). Implicit trustworthiness decisions: automatic coding of face properties in the human amygdala. *J Cogn Neurosci, 19*(9), 1508-1519.

Epley, N., & Waytz, A. (2010). Mind perception. In S. T. Fiske, D. T. Gilbert & G. Lindzey (Eds.), *Handbook of social psychology* (5th ed. ed.). New Jersey: John Wiley & Sons, Inc., Hoboken

Ethofer, T., Gschwind, M., & Vuilleumier, P. (2011). Processing social aspects of human gaze: a combined fMRI-DTI study. *Neuroimage, 55*(1), 411-419.

Evans, J. S. (2008). Dual-processing accounts of reasoning, judgment, and social cognition. *Annual Review of Psychology, 59*, 255-278.

Farroni, T., Csibra, G., Simion, F., & Johnson, M. H. (2002). Eye contact detection in humans from birth. *Proc Natl Acad Sci U S A, 99*(14), 9602-9605.

Frey, S. (1999). *Die Macht des Bildes*. Bern, Germany: Huber.

Frith, U. (2001). Mind blindness and the brain in autism. *Neuron, 32*(6), 969-979.

Frith, U. (2003). *Autism: Explaining the enigma.* Oxford: Basil Blackwell.

Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalizing. *Philos Trans R Soc Lond B Biol Sci, 358*(1431), 459-473.

Gerber, A. J., Posner, J., Gorman, D., Colibazzi, T., Yu, S., Wang, Z., et al. (2008). An affective circumplex model of neural systems subserving valence, arousal, and cognitive overlay during the appraisal of emotional faces. *Neuropsychologia, 46*(8), 2129-2139.

Gilbert, D. T., & Krull, D. S. (1988). Seeing less and knowing more: The benefits of perceptual ignorance. *Journal of Personality and Social Psychology, 54*(2), 193-202.

Gobbini, M. I., Koralek, A. C., Bryan, R. E., Montgomery, K. J., & Haxby, J. V. (2007). Two takes on the social brain: a comparison of theory of mind tasks. *J Cogn Neurosci, 19*(11), 1803-1814.

Grammer, K., Honda, M., Juette, A., & Schmitt, A. (1999). Fuzziness of nonverbal courtship communication unblurred by motion energy detection. *Journal of Personality and Social Psychology, 77*(3), 487-508.

Hains, S. M., & Muir, D. W. (1996). Infant sensitivity to adult eye direction. *Child Dev, 67*(5), 1940-1951.

Harris, L. T., Todorov, A., & Fiske, S. T. (2005). Attributions on the brain: neuro-imaging dispositional inferences, beyond theory of mind. *Neuroimage, 28*(4), 763-769.

Heeger, D. J., & Ress, D. (2002). What does fMRI tell us about neuronal activity? *Nat Rev Neurosci, 3*(2), 142-151.

Heider, F., & Simmel, M. (1944). An experimental study of apparent behavior. *Am. J. Psychol. , 57*, 243-259.

Hoffman, E. A., & Haxby, J. V. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nat Neurosci, 3*(1), 80-84.

Hood, B. M., Macrae, C. N., Cole-Davies, V., & Dias, M. (2003). Eye remember you: the effects of gaze direction on face recognition in children and adults. *Developmental Science, 6*(1), 67-71.

Klin, A. (2000). Attributing social meaning to ambiguous visual stimuli in higher-functioning autism and Asperger syndrome: The Social Attribution Task. *J Child Psychol Psychiatry, 41*(7), 831-846.

Klin, A., & Jones, W. (2006). Attributing social and physical meaning to ambiguous visual displays in individuals with higher-functioning autism spectrum disorders. *Brain Cogn, 61*(1), 40-53.

Klin, A., Jones, W., Schultz, R., & Volkmar, F. (2003). The enactive mind, or from actions to cognition: lessons from autism. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 358*(1430), 345-360.

Kraemer, N. C. (2008). Nonverbal communication. In J. J. Blascovich & C. R. Hartel (Eds.), *Human behavior in military contexts* (pp. 150-188). Washington: National Academic Press.

Kringelbach, M. L. (2005). The human orbitofrontal cortex: linking reward to hedonic experience. *Nat Rev Neurosci, 6*(9), 691-702.

Kuzmanovic, B., Bente, G., von Cramon, D. Y., Schilbach, L., Tittgemeyer, M., & Vogeley, K. (2012). Imaging first impressions: Distinct neural processing of verbal and nonverbal social information. *NeuroImage, 60*(1), 179-188.

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

Kuzmanovic, B., Schilbach, L., Georgescu, A. L., Kockler, H., Santos, N. S., Shah, J. N., et al. (under review). When seeing does not lead to feeling: Absent neural responses to increasing subjective animacy experience in high-functioning autism. *Social Cognitive and Affective Neuroscience*.

Kuzmanovic, B., Schilbach, L., Lehnhardt, F.-G., Bente, G., & Vogeley, K. (2011). A matter of words: Impact of verbal and nonverbal information on impression formation in high-functioning autism. *Research in Autism Spectrum Disorders, 5*, 604–613.

Liddell, B. J., Brown, K. J., Kemp, A. H., Barton, M. J., Das, P., Peduto, A., et al. (2005). A direct brainstem-amygdala-cortical 'alarm' system for subliminal signals of fear. *Neuroimage, 24*(1), 235-243.

Lieberman, M. D. (2007). Social cognitive neuroscience: a review of core processes. *Annu Rev Psychol, 58*, 259-289.

Lieberman, M. D. (2010). Social cognitive neuroscience. In S. T. Fiske, D. T. Gilbert & G. Lindzey (Eds.), *Handbook of Social Psychology* (5th ed., pp. 143-193). New York: McGraw Hill.

Logothetis, N. K., Pauls, J., Augath, M., Trinath, T., & Oeltermann, A. (2001). Neurophysiological investigation of the basis of the fMRI signal. *Nature, 412*(6843), 150-157.

Macrae, C. N., Hood, B. M., Milne, A. B., Rowe, A. C., & Mason, M. F. (2002). Are you looking at me? Eye gaze and person perception. *Psychol Sci, 13*(5), 460-464.

Maddock, R. J., Garrett, A. S., & Buonocore, M. H. (2003). Posterior cingulate cortex activation by emotional words: fMRI evidence from a valence decision task. *Hum Brain Mapp, 18*(1), 30-41.

Martin, A., & Weisberg, J. (2003). Neural foundations for understanding social and mechanical concepts. *Cogn Neuropsychol, 20*(3-6), 575-587.

Mason, M. F., Hood, B. M., & Macrae, C. N. (2004). Look into my eyes: gaze direction and person memory. *Memory, 12*(5), 637-643.

Mason, M. F., Tatkow, E. P., & Macrae, C. N. (2005). The look of love: gaze shifts and person perception. *Psychol Sci, 16*(3), 236-239.

Mitchell, J. P., Banaji, M. R., & Macrae, C. N. (2005). The link between social cognition and self-referential thought in the medial prefrontal cortex. *J Cogn Neurosci, 17*(8), 1306-1315.

Montgomery, D. E., Bach, L. M., & Moran, C. (1998). Children's use of looking behavior as a cue to detect another's goal. *Child Development, 69*, 692-705.

Ochsner, K. N., Beer, J. S., Robertson, E. R., Cooper, J. C., Gabrieli, J. D., Kihsltrom, J. F., et al. (2005). The neural correlates of direct and reflected self-knowledge. *Neuroimage, 28*(4), 797-814.

Pegna, A. J., Khateb, A., Lazeyras, F., & Seghier, M. L. (2005). Discriminating emotional faces without primary visual cortices involves the right amygdala. *Nat Neurosci, 8*(1), 24-25.

Pelphrey, K. A., Morris, J. P., & McCarthy, G. (2004). Grasping the intentions of others: the perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. *J Cogn Neurosci, 16*(10), 1706-1716.

Pelphrey, K. A., Singerman, J. D., Allison, T., & McCarthy, G. (2003). Brain activation evoked by perception of gaze shifts: the influence of context. *Neuropsychologia, 41*(2), 156-170.

Pelphrey, K. A., Viola, R. J., & McCarthy, G. (2004). When strangers pass: processing of mutual and averted social gaze in the superior temporal sulcus. *Psychol Sci, 15*(9), 598-603.

Pessoa, L. (2008). On the relationship between emotion and cognition. *Nat Rev Neurosci, 9*(2), 148-158.

Phan, K. L., Taylor, S. F., Welsh, R. C., Ho, S. H., Britton, J. C., & Liberzon, I. (2004). Neural correlates of individual ratings of emotional salience: a trial-related fMRI study. *Neuroimage, 21*(2), 768-780.

Phelps, E. A., O'Connor, K. J., Cunningham, W. A., Funayama, E. S., Gatenby, J. C., Gore, J. C., et al. (2000). Performance on indirect measures of race evaluation predicts amygdala activation. *J Cogn Neurosci, 12*(5), 729-738.

Posner, J., Russell, J. A., Gerber, A., Gorman, D., Colibazzi, T., Yu, S., et al. (2009). The neurophysiological bases of emotion: An fMRI study of the affective circumplex using emotion-denoting words. *Hum Brain Mapp, 30*(3), 883-895.

Puce, A., Allison, T., Bentin, S., Gore, J. C., & McCarthy, G. (1998). Temporal cortex activation in humans viewing eye and mouth movements. *J Neurosci, 18*(6), 2188-2199.

Raichle, M. E., & Mintun, M. A. (2006). Brain work and brain imaging. *Annu Rev Neurosci, 29*, 449-476.

Ramachandran, R., Mitchell, P., & Ropar, D. (2009). Do individuals with autism spectrum disorders infer traits from behavior? *The Journal of Child Psychology and Psychiatry, 50*(7), 871-878.

Rauch, S. L., Whalen, P. J., Shin, L. M., McInerney, S. C., Macklin, M. L., Lasko, N. B., et al. (2000). Exaggerated amygdala response to masked facial stimuli in posttraumatic stress disorder: a functional MRI study. *Biol Psychiatry, 47*(9), 769-776.

Robinson, J. L., Laird, A. R., Glahn, D. C., Lovallo, W. R., & Fox, P. T. (2010). Metaanalytic connectivity modeling: delineating the functional connectivity of the human amygdala. *Hum Brain Mapp, 31*(2), 173-184.

Rule, N. O., Moran, J. M., Freeman, J. B., Whitfield-Gabrieli, S., Gabrieli, J. D., & Ambady, N. (2011). Face value: amygdala response reflects the validity of first impressions. *Neuroimage, 54*(1), 734-741.

Said, C. P., Baron, S. G., & Todorov, A. (2009). Nonlinear amygdala response to face trustworthiness: contributions of high and low spatial frequency information. *J Cogn Neurosci, 21*(3), 519-528.

Sander, D., Grafman, J., & Zalla, T. (2003). The human amygdala: an evolved system for relevance detection. *Reviews in the Neurosciences 14*(4), 303-316.

Santos, N. S., David, N., Bente, G., & Vogeley, K. (2008). Parametric induction of animacy experience. *Conscious Cogn, 17*(2), 425-437.

Santos, N. S., Kuzmanovic, B., David, N., Rotarska-Jagiela, A., Eickhoff, S. B., Shah, J. N., et al. (2010). Animated brain: a functional neuroimaging study on animacy experience. *Neuroimage, 53*(1), 291-302.

Schilbach, L., Eickhoff, S. B., Cieslik, E. C., Kuzmanovic, B., & Vogeley, K. (2011). Shall we do this together? Social gaze influences action control in a comparison group, but not in individuals with high-functioning autism. *Autism*.

Schilbach, L., Wilms, M., Eickhoff, S. B., Romanzetti, S., Tepest, R., Bente, G., et al. (2010). Minds made for sharing: initiating joint attention recruits reward-related neurocircuitry. *J Cogn Neurosci, 22*(12), 2702-2715.

Schiller, D., Freeman, J. B., Mitchell, J. P., Uleman, J. S., & Phelps, E. A. (2009). A neural mechanism of first impressions. *Nat Neurosci, 12*(4), 508-514.

Schultz, R. T., Gauthier, I., Klin, A., Fulbright, R. K., Anderson, A. W., Volkmar, F., et al. (2000). Abnormal ventral temporal cortical activity during face discrimination among individuals with autism and Asperger syndrome. *Archives of General Psychiatry, 57*(4), 331-340.

Schultz, R. T., Grelotti, D. J., Klin, A., Kleinman, J., Van der Gaag, C., Marois, R., et al. (2003). The role of the fusiform face area in social cognition: implications for the pathobiology of autism. *Philos Trans R Soc Lond B Biol Sci, 358*(1430), 415-427.

Schwartz, C., Bente, G., Gawronski, A., Schilbach, L., & Vogeley, K. (2010). Responses to nonverbal behaviour of dynamic virtual characters in high-functioning autism. *Journal of Autism and Developmental Disorders, 40*(1), 100-111.

Senju, A., & Hasegawa, T. (2005). Direct gaze captures visuospatial attention. *Visual Cognition, 12*(1), 127-144.

Senju, A., & Johnson, M. H. (2009). The eye contact effect: mechanisms and development. *Trends Cogn Sci, 13*(3), 127-134.

Senju, A., Southgate, V., White, S., & Frith, U. (2009). Mindblind eyes: an absence of spontaneous theory of mind in Asperger syndrome. *Science, 325*(5942), 883-885.

Sergerie, K., Chochol, C., & Armony, J. L. (2008). The role of the amygdala in emotional processing: a quantitative meta-analysis of functional neuroimaging studies. *Neurosci Biobehav Rev, 32*(4), 811-830.

Smith, A. D., Hood, B. M., & Hector, K. (2006). Eye remember you two: gaze direction modulates face recognition in a developmental study. *Dev Sci, 9*(5), 465-472.

Spengler, S., Bird, G., & Brass, M. (2010). Hyperimitation of actions is related to reduced understanding of others' minds in autism spectrum conditions. *Biol Psychiatry, 68*(12), 1148-1155.

Tavares, P., Lawrence, A. D., & Barnard, P. J. (2008). Paying attention to social meaning: an FMRI study. *Cereb Cortex, 18*(8), 1876-1885.

Todorov, A. (2008). Evaluating faces on trustworthiness: an extension of systems for recognition of emotions signaling approach/avoidance behaviors. *Ann N Y Acad Sci, 1124*, 208-224.

Todorov, A., & Engell, A. D. (2008). The role of the amygdala in implicit evaluation of emotionally neutral faces. *Soc Cogn Affect Neurosci, 3*(4), 303-312.

Todorov, A., Gobbini, M. I., Evans, K. K., & Haxby, J. V. (2007). Spontaneous retrieval of affective person knowledge in face perception. *Neuropsychologia, 45*(1), 163-173.

Uleman, J. S., Adil Saribay, S., & Gonzalez, C. M. (2008). Spontaneous inferences, implicit impressions, and implicit theories. *Annual Review of Psychology, 59*, 329-360.

Ungerleider, L. G., & Haxby, J. V. (1994). 'What' and 'where' in the human brain. *Curr Opin Neurobiol, 4*(2), 157-165.

Van Overwalle, F., & Baetens, K. (2009). Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. *Neuroimage, 48*(3), 564-584.

Vogeley, K., Bussfeld, P., Newen, A., Herrmann, S., Happe, F., Falkai, P., et al. (2001). Mind reading: neural mechanisms of theory of mind and self-perspective. *Neuroimage, 14*(1 Pt 1), 170-181.

von Grunau, M., & Anston, C. (1995). The detection of gaze direction: a stare-in-the-crowd effect. *Perception, 24*(11), 1297-1313.

Vuilleumier, P., George, N., Lister, V., Armony, J., & Driver, J. (2005). Effects of perceived mutual gaze and gender on face processing and recongnition memory. *Visual Cognition, 12*(1), 85-101.

Walter, H., Adenzato, M., Ciaramidaro, A., Enrici, I., Pia, L., & Bara, B. G. (2004). Understanding intentions in social interaction: the role of the anterior paracingulate cortex. *J Cogn Neurosci, 16*(10), 1854-1863.

Watzlawick, P., Bavelas, J. H., & Jackson, D. D. (1967). *Pragmatics of human communication: A study of interactional patterns, pathologies, and paradoxes*: New York, Norton

Whalen, P. J., Kagan, J., Cook, R. G., Davis, F. C., Kim, H., Polis, S., et al. (2004). Human amygdala responsivity to masked fearful eye whites. *Science, 306*(5704), 2061.

Whalen, P. J., Rauch, S. L., Etcoff, N. L., McInerney, S. C., Lee, M. B., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *J Neurosci, 18*(1), 411-418.

Wheatley, T., Milleville, S. C., & Martin, A. (2007). Understanding animate agents: distinct roles for the social network and mirror system. *Psychol Sci, 18*(6), 469-474.

Winston, J. S., Strange, B. A., O'Doherty, J., & Dolan, R. J. (2002). Automatic and intentional brain responses during evaluation of trustworthiness of faces. *Nat Neurosci, 5*(3), 277-283.

Zaki, J., Hennigan, K., Weber, J., & Ochsner, K. N. (2010). Social cognitive conflict resolution: contributions of domain-general and domain-specific neural systems. *J Neurosci, 30*(25), 8481-8488.

Zald, D. H. (2003). The human amygdala and the emotional evaluation of sensory stimuli. *Brain Res Brain Res Rev, 41*(1), 88-123.

Zysset, S., Huber, O., Ferstl, E., & von Cramon, D. Y. (2002). The anterior frontomedian cortex and evaluative judgment: an fMRI study. *Neuroimage, 15*(4), 983-991.

Zysset, S., Huber, O., Samson, A., Ferstl, E. C., & von Cramon, D. Y. (2003). Functional specialization within the anterior medial prefrontal cortex: a functional magnetic resonance imaging study with human subjects. *Neurosci Lett, 335*(3), 183-186.

NeuroImage 46 (2009) 1154–1163

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Duration matters: Dissociating neural correlates of detection and evaluation of social gaze

Bojana Kuzmanovic [a,*], Alexandra L. Georgescu [a], Simon B. Eickhoff [b,c,g], Nadim J. Shah [b,d], Gary Bente [e], Gereon R. Fink [b,d,f], Kai Vogeley [a,d]

[a] *Department of Psychiatry and Psychotherapy, University of Cologne, Germany*
[b] *Institute of Neurosciences and Medicine, Research Center Juelich, Germany*
[c] *Department of Psychiatry and Psychotherapy, RWTH Aachen University, Germany*
[d] *Brain Imaging Center West, Research Center Juelich, Germany*
[e] *Department of Psychology, University of Cologne, Germany*
[f] *Department of Neurology, University of Cologne, Germany*
[g] *JARA (Jülich Aachen Research Alliance), Translational Brain Medicine, Germany*

ARTICLE INFO

Article history:
Received 30 October 2008
Revised 20 February 2009
Accepted 12 March 2009
Available online 25 March 2009

Keywords:
Gaze duration
Gaze direction
Mentalizing
Reward
Orbitofrontal cortex
Paracingulate cortex
fMRI

ABSTRACT

The interpretation of interpersonal gaze behavior requires the use of complex cognitive processes and guides social interactions. Among a variety of different gaze characteristics, gaze direction and gaze duration modulate crucially the meaning of the “social gaze”. Nevertheless, prior neuroimaging studies disregarded the relevance of gaze duration by focusing on gaze direction only.

The present functional magnetic resonance imaging (fMRI) study focused on the differentiation of these two gaze parameters. Therefore direct gaze displayed by virtual characters was contrasted with averted gaze and, additionally, systematically varied with respect to gaze duration (i.e., 1, 2.5 or 4 s). Consistent with prior findings, behavioral data showed that likeability was higher for direct than for averted gaze and increased linearly with increasing direct gaze duration. On the neural level, distinct brain regions were associated with the processing of gaze direction and gaze duration: (i) the comparison between direct and averted gaze revealed activations in bilateral occipito-temporal regions including the posterior superior temporal sulcus (pSTS); (ii) whereas increasing duration of direct gaze evoked differential neural responses in the medial prefrontal cortex (MPFC) including orbitofrontal and paracingulate regions.

The results suggest two complementary cognitive processes related to different gaze parameters. On the one hand, the recruitment of multimodal sensory regions in the pSTS indicates *detection* of *gaze direction* via complex visual analysis. On the other hand, the involvement of the MPFC associated with outcome monitoring and mentalizing indicates higher-order social cognitive processes related to *evaluation* of the ongoing communicational input conveyed by direct *gaze duration*.

Introduction

Everyday experience as well as extensive research in psychology and social cognitive neuroscience confirm the pivotal role of human gaze in social interactions and its impact on cognitive, affective and motivational processes (Argyle and Cook, 1976; Gueguen and Jacob, 2002; Hood and Macrae, 2007; Vuilleumier and Pourtois, 2007). “Social gaze” might be metaphorically considered as glue in interpersonal communication as it allows not only for the coordination of attention and activities (Argyle and Cook, 1976) but also influences our social perception and the evaluation of others (Argyle et al., 1974; Kleinke, 1986; Mason et al., 2005; Mirenda et al., 1983). Moreover, understanding the ostensive function of eye gaze is closely linked to the ability to infer mental states of others (Baron-Cohen, 1995; Eskritt and Lee, 2007), a cognitive process that is usually referred to as “Theory of Mind” (Premack and Woodruff, 1978) or “mentalizing” (Frith, 2001). On the one hand, during earlier years of human ontogeny, recognizing that people can perceive an event differently depending on their gaze directions may aid in overcoming the initial egocentric perspective and in understanding of mind in general (Gopnik et al., 1994). On the other hand, more sophisticated knowledge about the relations and causes of mental states could help interpret eye gaze information at later ages (Eskritt and Lee, 2007). Thus, both the capacity to understand the eye gaze and to infer mental states influence each other's developments resulting in an automatic association between a particular gaze behavior and the intention “behind” it.

---

[*] Corresponding author. Fax: +0049 221 478 87702.
E-mail address: bojana.kuzmanovic@uk-koeln.de (B. Kuzmanovic).

1053-8119/$ – see front matter © 2009 Elsevier Inc. All rights reserved.
doi:10.1016/j.neuroimage.2009.03.037

Particularly in the context of direct gaze, i.e. when a person is looking straight into the eyes of another person, mentalizing processes are likely to come into play. As a nonverbal signal of notable salience (Gibson and Pick, 1963; von Grunau and Anston, 1995), direct gaze can be used to initiate communication by indicating "self-reference" and by conveying interpersonal attitudes (Kampe et al., 2003; Kleinke, 1986; Mirenda et al., 1983; Valentine and Ehrlichman, 1979; Wicker et al., 1998). Here, self-reference connotes that a person (the sender) transfers an intention to communicate by looking directly at someone (a receiver). The receiver, in turn, must be able to understand this intention and to recognize that he/she is addressed, thus experiencing that the direct gaze refers to him/her. In this case, direct gaze would be "more than a trivial sensory experience" thereby triggering further reasoning about the meaning of and the motives for the other's messages as well as about the appropriateness of one's own response (Wicker et al., 1998).

Converging neuroimaging evidence has demonstrated that processing of gaze as a component of biological motion is consistently associated with activation in the posterior superior temporal sulcus (pSTS) (Akiyama et al., 2006; Hoffman and Haxby, 2000; Hooker et al., 2003; Pelphrey et al., 2004b; Puce et al., 1998; Wicker et al., 1998). Moreover, direct gaze in particular has been shown to recruit additional neural regions associated with complex social cognitive processing including the amygdala, the fusiform gyrus and the prefrontal cortex (Conty et al., 2007; George et al., 2001; Kawashima et al., 1999; Wicker et al., 2003). For instance, Kampe et al. (2003) showed that direct gaze (compared to averted gaze) elicited activation in the paracingulate part of the medial prefrontal cortex (MPFC). Interestingly, neuroimaging studies consistently suggest a special role of the MPFC in social cognition (Amodio and Frith, 2006). Within this region, functional divisions were defined differentiating between the orbitofrontal cortex (OFC) that is related to monitoring the reward value of stimuli and possible outcomes (Amodio and Frith, 2006; Kringelbach, 2005) and the above mentioned paracingulate cortex (PCC) commonly involved in mentalizing and self-referential processing (Gallagher et al., 2002; Gobbini et al., 2007; Mitchell et al., 2005; Ochsner et al., 2005; Vogeley et al., 2001; Walter et al., 2004). Thus, the result reported by Kampe et al. (2003) confirms the proposed link between direct gaze and understanding self-relevant intentions of others. Furthermore, differential involvement of the MPFC during processing of direct gaze has also been observed in combination with communicative facial expressions (Schilbach et al., 2006). However, the majority of previous neuroimaging studies on direct gaze, independent of facial expression, were unable to demonstrate the specific role of the MPFC during the processing of gaze-related information (George et al., 2001; Hoffman and Haxby, 2000; Wicker et al., 1998). For instance, a functional magnetic resonance imaging (fMRI) study by Calder et al. (2002) even reported that the MPFC was primarily engaged in the processing of averted, rather than direct gaze.

The lack of unequivocal evidence with respect to MPFC recruitment during the processing of context-free and neutral direct gaze could be attributed to the confinement to rather simplistic, categorical experimental designs using static stimulus material and considering only *gaze direction*. However, in everyday human interactions, the interpretation of gaze behavior appears to depend crucially on subtle, dynamic parameters, among which *gaze duration* represents a prominent example (Argyle et al., 1974; Brooks et al., 1986; Droney and Brooks, 1993; Gueguen and Jacob, 2002; Knackstedt and Kleinke, 1991; Montgomery et al., 1998). Previous behavioral studies have demonstrated that the longer a person looked straight into the observer's eyes, the more favorably this person was judged with regard to likeability, potency and self-esteem (Argyle et al., 1974; Brooks et al., 1986; Droney and Brooks, 1993; Knackstedt and Kleinke, 1991). Along the same line, Gueguen and Jacob (2002) were able to show that, when direct gaze was maintained, pedestrians were more likely to participate in an intercept survey. Argyle and Cook (1976) explain these results by postulating that in a social interaction prolonged gaze can convey approach signals including the need for feedback or affiliative needs. The receiver, in turn, may experience these signals as rewarding and could reciprocate them by evaluating the gazing person more positively and by adapting one's own behavior. Thereby, these approach forces "behind" the direct gaze motivate and guide interpersonal behavior and influence the perception and evaluation of others. However, prolonged direct gaze does not solely convey rewarding aspects like social attention and interest (Mason et al., 2005), but may also comprise avoidance components including the demonstration of dominance and the fear of revealing inner states (Argyle and Dean, 1965). As a consequence of this ambiguity, changing gaze signals require continuous decoding for the purpose of effective outcome monitoring.

Furthermore, it could be demonstrated that gaze duration as compared to gaze direction represents a more complex source of social information because it requires more sophisticated mentalizing abilities in order to perform an adequate interpretation (Eskritt and Lee, 2007). In tasks requiring inferences about other's desires from the simple detection of eye direction, 4-year olds were already successful (Baron-Cohen, 1995). However, advanced levels of understanding gaze cues based on their relative duration were not yet present at this age (Montgomery et al., 1998). In contrast, the performance of 5- and 6-year olds was comparable to that of adults, indicating that during later developmental stages relative gaze duration towards different test objects can be efficiently used to infer others' preferences (Einav and Hood, 2006; Montgomery et al., 1998).

In spite of the behaviorally well established relevance of gaze duration for impression formation and motivation in social contexts, to the best of our knowledge, no fMRI study has yet focused on the neural correlates of this parameter. Thus, the aim of the present study was to investigate neural correlates of both the direction and the duration of the interpersonal gaze. We expect that the greater amount of social information inherent in varying the duration of the direct gaze as compared to simply contrasting the direct and the averted gaze direction would enclose the involvement of more complex social cognitive processes. Thus, we performed the present fMRI study to analyze whether systematically varying the duration of direct gaze significantly modulates its neural correlates. In the context of a person judgment task, virtual characters that initially displayed averted gaze and subsequently shifted their gaze towards the participant were presented. After a systematically varied amount of time (i.e., 1 s, 2.5 s or 4 s), gaze was shifted back to the initial, averted position. Additionally, a control condition without a gaze shift towards the participant, i.e. consisting solely of averted gaze, was presented. Given that the communicative intention conveyed by direct gaze has been conjectured to automatically and implicitly trigger the mentalizing mechanism (Kampe et al., 2003), no explicit instruction to infer mental states was given but participants were asked to rate the likeability of the stimulus faces after each trial. Predicted on the link between duration-sensitive gaze processing and understanding interpersonal intentions we hypothesize a direct gaze duration (DGd) related involvement of the PCC. Furthermore, we seek to confirm the proposed reward value of increasing DGd by replicating a more positive person evaluation on the behavioral level and by demonstrating differential responses in the OFC as a function of prolonged direct gaze. On the other hand, for the simple comparison between directed and averted gaze directions we expect the involvement of temporal regions including the STS as reported in previous neuroimaging studies in this field. In sum, as the continuous monitoring of DGd provides access to an additional source of social information, changes in the DGd should have a discriminative value for the recruitment of the MPFC including the OFC and the PCC.

Methods

Subjects

22 participants [12 male, 10 female; mean age 27.2 ± 3.9 (SD) years] with no history of neurological or psychiatric illness gave informed consent and participated in the fMRI study. All participants were naïve with respect to the experimental task and the purpose of the study. Right-handedness was confirmed by the Edinburgh Inventory for Handedness (Oldfield, 1971). The study was approved by the local ethics committee of the Medical Faculty of the University of Cologne.

Stimulus material and experimental design

Due to the advantage of systematic manipulability, which is an important prerequisite for investigating subtle nonverbal signals such as gaze duration, we applied computer-generated virtual characters as stimulus material. In particular, the systematic modification of facial characteristics provided an effective countermeasure for confounding influences such as face morphology and non-intended mimicry movements. The advantages of using computer-animated characters for experimental communication research have been already stressed at an early stage of research (Bente, 1989; Bente et al., 1996; Blascovich et al., 2002) issuing tailorable research instrumentation for various applications. In this line, a series of studies have consistently confirmed the potential of virtual characters to elicit social impressions comparable to video recordings of real people (Bente et al., 2001a,b) and to even mediate the experience of social presence, i.e. of being with another person (Bailenson et al., 2003; Ku et al., 2005). Finally, recent research demonstrated that facial animations of virtual characters evoke brain responses comparable to those evoked by real human faces (Moser et al., 2007).

Using the 3D software package Poser 6 (Curious Lab®), 32 male and 32 female faces displaying a neutral emotional expression have been designed by systematically varying each of five face parameters (mouth, nose, cheeks, cheekbones, hair color) on two levels. Subsequently, the likeability of these stimuli was evaluated in a pilot study with nine healthy participants [mean age 22.8 ± 3.8 (SD) years]. Based on this pilot evaluation, 10 male and 10 female equally and moderately likeable faces (mean likeability rating 2.68, ranging from 2.5 to 2.78, assessed on a four-point likeability rating scale consisting of following response options: 1 = very dislikable, 2 = rather dislikable, 3 = rather likeable, 4 = very likeable) were selected for the further use in the fMRI study to prevent confounding effects of general attractiveness. In the next step, we created animations of the selected faces performing strictly controlled gaze behavior. Each face initially displayed an averted gaze followed by a short eye blink (150 ms) and a direct gaze and finally shifted the gaze back to the initial, averted position (direct gaze condition, DG; see Fig. 1, C). Thereby, the duration of the direct gaze was parametrically varied on three levels: 1 s, 2.5 s and 4 s. The duration of the initial and final averted gaze was adjusted according to the respective duration of the direct gaze in order to establish an equal total duration of 5650 ms for all animations. For example, in trials with direct gaze duration of 2500 ms the averted gaze sequences lasted for 1500 ms each [direct gaze (2500 ms) + 2 * averted gaze (1500 ms) + eye blink (150 ms) = 5650 ms]. The preceding eye blink was implemented to increase ecological validity of the stimuli by a more naturalistic gaze behavior (Omori and Miyata, 2001). Additionally, animations with faces only displaying an averted gaze without switching to the direct gaze were generated to be included as a control condition (averted gaze condition, AG; see Fig. 1, B). In order to keep these events as close as possible to those of the direct gaze condition, the eye blink also occurred in control trials. The timing of this blink was randomly chosen from the three blinks preceding direct gaze. The control condition AG was necessary to allow the characterization of the main effect of direct gaze by comparing events with direct and averted gaze thereby considering the gaze direction only. The events with averted gaze were not varied with respect to duration resulting in an unbalanced experimental design with two factors, namely gaze direction and gaze duration. The categorical factor gaze direction was varied on two levels, namely AG and DG. The parametric factor gaze duration was systematically varied only within the DG condition on three levels (see Fig. 1, A).

Finally, to take the greater salience of the direct gaze in deviated head orientation into account (Vuilleumier et al., 2005), stimulus faces were shown with two different head orientations — slightly turned to the left or right side. Across all trials, the averted gaze was kept congruent to the head orientation (e.g., right gaze direction when right head orientation was presented).

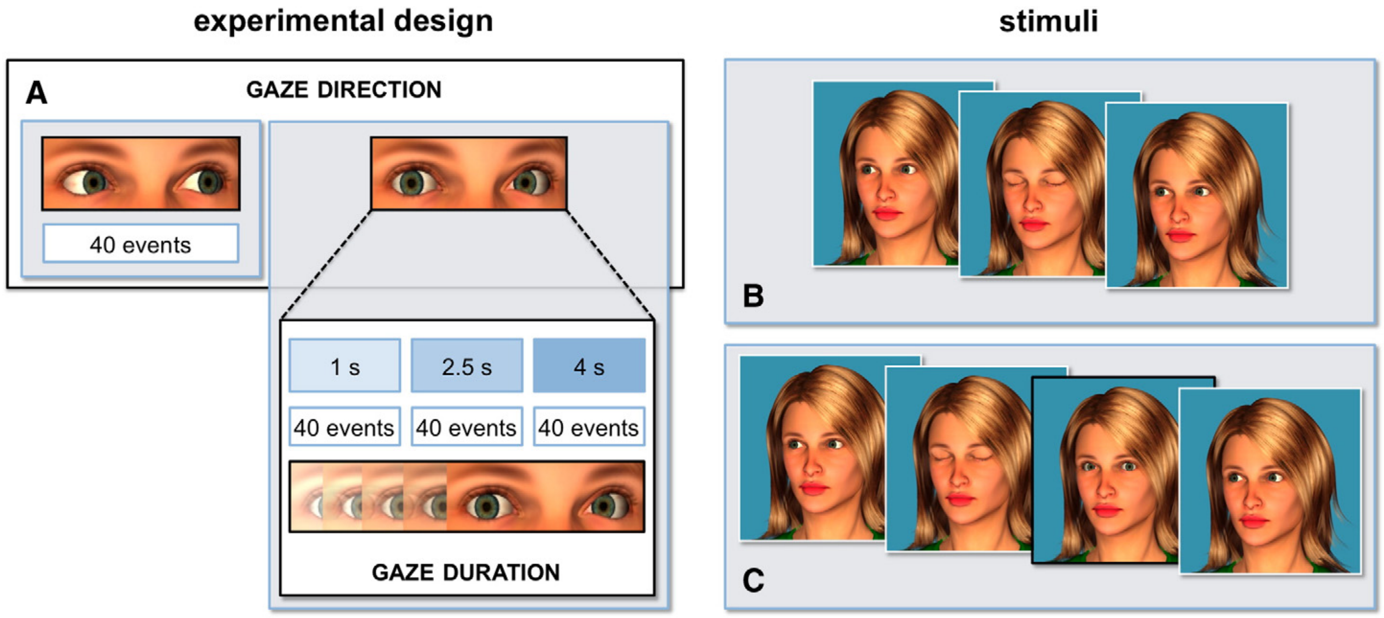

Fig. 1. Experimental design and stimuli. (A) We focused on (i) the main effect of gaze direction (direct gaze vs. averted gaze); and (ii) the main effect of gaze duration (parametric modulation of the direct gaze processing by corresponding gaze durations). (B) Time course of an animation of a stimulus face displaying averted gaze. (C) Time course of an animation of a stimulus face displaying direct gaze. The duration of the direct gaze (highlighted by a black frame) was varied systematically (1000 ms, 2500 ms or 4000 ms); the duration of averted gaze was adapted accordingly (2 * 2250 ms, 1500 ms or 750 ms) so that each stimulus lasted for 5650 ms in total (including a short eye blink of 150 ms).

The stimulus presentation and response recording was performed by the software package Presentation (version 11.3; Neurobehavioral Systems, Inc., www.neurobs.com/). Visual stimulation was provided through magnet-compatible goggles (VisuaStim™, Resonance Technology, CA, USA) and responses were assessed using four buttons of a MR-compatible response device (LUMItouch™, Photon Control Inc., BC, Canada). Due to technical difficulties with the recording hardware, eye tracking could not be performed reliably and eye movements could hence not be considered in the present experiment. An experimental trial consisted of a stimulus presentation followed by a likeability rating scale lasting for 1000 ms. Further, each trial entailed two randomly jittered inter-stimulus intervals (ISIs): one between each stimulus presentation and the following rating scale in order to enable for statistical isolation and an independent analysis of the person perception and the response (applied ISI durations: 1500 ms, 1750 ms, 2250 ms and 2500 ms; mean ISI 2000 ms) and the other between single trials to increase condition-specific BOLD signal discriminability (Dale, 1999; Serences, 2004) (applied ISI durations: 5400 ms, 6300 ms, 7200 ms and 8100 ms; mean ISI 6750 ms). Taken together, an average trial lasted for 15400 ms. Each of the twenty stimulus faces was presented with two repetitions (head orientation towards right or left side) for each of four gaze conditions (DG lasting for 1 s, 2.5 s or 4 s and AG), summing up to a total of 160 trials. The experiment was conducted in an event-related fashion and split into two runs each lasting for 20 min. Participants were asked to perform one run with their right and the other with their left hand in order to balance for lateralized motor-related activations. Both runs consisted of equivalent numbers of condition-specific events, shown in randomized order. The sequence of the two runs was randomized as well. Prior to the fMRI experiment participants were familiarized with the performance of the task in a standardized instruction and practice session presented on a computer screen outside the magnet. None of the stimulus faces used in this introduction was used in the subsequent fMRI experiment. Participants were asked to pay attention to the presented animated faces and to evaluate each of them on a four-point likeability rating scale consisting of following response options: 1 = very dislikable, 2 = rather dislikable, 3 = rather likeable, 4 = very likeable. They were instructed to respond as spontaneously and quickly as possible after the display of the rating scale. No explicit instructions were given about the dimension on which to base their likeability judgments.

Functional magnetic resonance imaging

Functional and structural magnetic resonance images were acquired on a Siemens Trio 3.0 T whole-body scanner (Siemens Medical Solutions, Erlangen, Germany). For the fMRI scans we used T2*-weighted gradient echo planar imaging (EPI) sequence with following imaging parameters: TR = 2200 ms, TE = 30 ms, field of view = 200×200 mm^2, 36 axial slices, slice thickness = 3.0 mm, in-plane resolution = 3.1×3.1 mm^2. Each session consisted of 574 images preceded by 4 additional images allowing for T1 magnetic saturation effects. These 4 images were discarded prior to further image processing. The slices approximately covered the whole brain omitting only minimal sections of the most superior part of the parietal cortex and the most inferior part of the cerebellum. For the structural images we used high-resolution T1-weighted magnetization-prepared rapid acquisition gradient echo (MPRAGE) sequence with the following parameters: TR = 2250 ms, TE = 3.93 ms, field of view = 256×256 mm^2, 176 sagittal slices, slice thickness = 1.0 mm, in-plane resolution = 1.0×1.0 mm^2.

Imaging data processing

Preprocessing

Images were analyzed using MATLAB 6.5 (The Mathworks Inc., Natick, USA) and the Statistical Parametric Mapping software package (SPM5; Wellcome Department of Imaging Neuroscience, London, UK) as follows. The EPI images were corrected for head movements between scans by an affine registration (Ashburner and Friston, 2003). For realignment we used a two-step procedure, by which images were initially realigned to the first image of the time series and subsequently re-realigned to the mean of all images after the first step. After completing the realignment, the mean EPI image for each participant was computed and spatially normalized to the MNI single subject template (Collins et al., 1994; Evans et al., 1992; Holmes et al., 1998) using the “unified segmentation” function in SPM5. The ensuing deformation was subsequently applied to the individual EPI volumes as well as to the T1 scan, which was coregistered to the mean of the realigned EPI volumes beforehand. The normalized images were spatially smoothed using an 8 mm FWHM Gaussian kernel to meet the statistical requirements of further analysis and to compensate for macroanatomical variations across participants.

Statistical analysis

The data were analyzed using a General Linear Model as implemented in SPM5. Two separate analyses of the imaging data were performed. For both analyses presented here, events were defined by onsets and durations of corresponding stimulus face presentations, whereas durations were always amounted to 5650 ms according to the time the virtual character was present. All response events were modeled on separate regressors (rR for responses with the right hand and rL for responses with the left hand), whereby the duration of all response events was amounted to 1000 ms according to the time the rating scale was present. Head movement estimates were included as confounds to exclude movement-related variance from the image time series. Low-frequency signal drifts were filtered using a cutoff period of 128 s.

Analysis 1 followed a combined categorical-parametric design that allowed us to characterize different forms of responses to direct gaze: (i) categorical response to the presence of direct gaze, irrespective of duration, compared to averted gaze; and (ii) parametric response to varying gaze duration within the direct gaze condition by identifying brain regions where activations increase linearly with increasing DGd. At the single subject level, conditions DG and AG were modeled separately using a boxcar reference vector convolved with the canonical hemodynamic response function. Within this categorical framework, the effect of gaze duration (DGd) was modeled as a linear parametric modulation of the hemodynamic response to DG by the corresponding duration (1, 2.5 or 4 s). That is, for each single DG event both (i) the onset was defined within the regressor representing the categorical presence of the direct gaze; and (ii) a value for the length of the corresponding direct gaze (values: 1, 2.5 or 4) was specified within a modulatory regressor. In contrast to DG, AG was not parametrically modulated as there was no temporal variation in any respect. Taken together, two types of events (AG, DG) and one event parameter of interest (DGd) were included in the statistical analysis at the single subject level. In addition, response events rR and rL were included as well. For each participant, the following four contrasts were specified: (i) AG; (ii) DG; (iii) DGd; and (iv) rR and rL. Thereby, all events were computed against resting baseline by weighting only the regressor corresponding to that particular event with 1 and all other regressors weighted with 0. Only in the case of response events, both rR and rL regressors were weighted with 1. The single subject contrasts were then fed into the second-level group analysis using a flexible factorial ANOVA (factors: condition and subject), employing a random-effects model (Penny and Holmes, 2003). On the group level, differences between conditions and significant deviations from zero, respectively, were assessed by linear contrasts on the second-level parameter estimates thresholded at $p_c < 0.05$ at the cluster-level, corrected for multiple comparisons and at $p < 0.001$ at the voxel-level, uncorrected (Friston et al., 1996). The following t-contrasts were computed: (i) DG > AG (applied weightings: DG = 1, AG = −1); (ii) AG > DG (applied weightings: DG = −1, AG = 1); (iii) DGd (applied weightings: DGd = 1).

Within the analysis 1 we conducted an anatomically defined region of interest (ROI) analysis to investigate whether in addition to the mOFC (see Results and Discussion) subcortical striatal regions strongly implicated in reward-related processing (Kim et al., 2007; Liu et al., 2007; O'Doherty, 2004) exhibited similar DGd-sensitive hemodynamic responses. Using the automated atlas-based masking technique interfaced in SPM5 (Maldjian et al., 2003) we generated a ROI mask including the bilateral caudate nucleus, putamen and globus pallidus in reference to atlas volumes described in Lancaster et al. (2000). Within this ROI we computed the DGd-contrast thresholded at $p_c<0.05$ (family wise error [FWE]-corrected for multiple comparisons at the voxel-level).

Finally, in the supplementary analysis 2, we employed a categorical design where every DGd condition was modeled as a separate regressor. Here, four events of interest were included in the statistical analysis at the single subject level: (i) AG; (ii) direct gaze events with a duration of 1 s (DG1); (iii) direct gaze events with a duration of 2.5 s (DG2.5); and (iv) direct gaze events with a duration of 4 s (DG4). In addition, the response events rR and rL were included as well. This procedure allowed us to conduct pair-wise comparisons between single direct gaze conditions (e.g. DG4>DG1, DG1>DG4, etc.) in order to corroborate the results of the parametric analysis 1. Furthermore, this model enabled a more detailed characterization of activation patterns based on ensuing parameter estimates for each level of the DGd at a particular location of interest. Resulting contrast images at the first-level of analysis 2 were: (i) AG; (ii) DG1; (iii) DG2.5; (iv) DG4; and (v) rR and rL. Contrast weightings for single subject level of the analysis 2 were performed as described for the analysis 1. These contrasts were included in the group level analysis where all possible comparisons between DG1, DG2.5 and DG 4 resulting in t-contrasts were computed. For instance, for the DG1>DG2.5-contrast the DG1-regressor was weighted with 1 and the DG2.5-regressor with -1. On the group level of the analysis, differences between conditions were assessed by linear contrasts on the second-level parameter estimates thresholded at $p_c<0.05$ at the cluster-level, corrected for multiple comparisons and at $p<0.001$ at the voxel-level, uncorrected (Friston et al., 1996).

Functional activations were anatomically localised by using the SPM anatomy toolbox, version 1.5 (Eickhoff et al., 2007; Eickhoff et al., 2005), implementing a maximum probability map. This map denotes the most likely anatomical area at each voxel of the MNI single subject template based on probabilistic cytoarchitectonic maps derived from the analysis of cortical areas in a sample of 10 human post-mortem brains, which were subsequently normalized to the MNI reference space (Eickhoff et al., 2006). For the purpose of additional anatomical precision, group contrasts were overlaid on a surface based representation of the MNI canonical brain using the SPM surfrend toolbox (written by I. Kahn; http://spmsurfrend.sourceforge.net). The surfaces were than rendered using NeuroLens (written by Dr. R. Hoge; http://neurolens.org).

Results

Behavioral results

The effect of DGd on likeability ratings was tested by a one-way repeated measures analysis of variance (ANOVA). The trials with purely averted gaze were excluded from this analysis as their primary purpose was to provide a control condition for the fMRI paradigm. Nevertheless, pair-wise comparisons revealed that likeability ratings for faces showing averted gaze were significantly lower than those for all direct gaze conditions (AG vs. DG1: $p_c=.004$; AG vs. DG2.5: $p_c=.003$; AG vs. DG4: $p_c=.002$, Bonferroni corrected). Thus, the ANOVA included three within subject independent variables, namely DG1, DG2.5 and DG4, and the dependent variable likeability ratings.

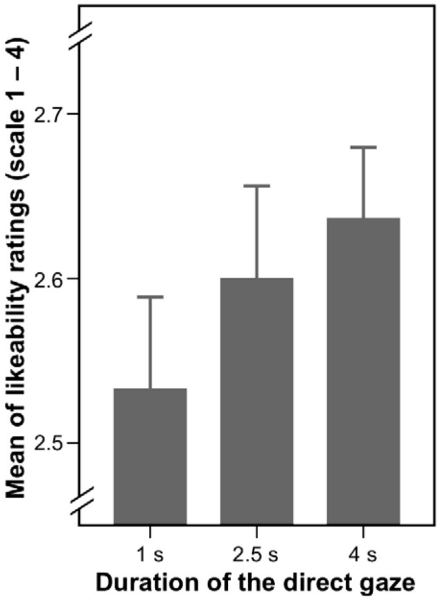

Fig. 2. The plot illustrates the significant main effect of direct gaze duration on likeability ratings. The scales on the y-axis indicate the mean of stimuli ratings. A score of 1 refers to rating a face as "very dislikable" and a one of 4 as "very likeable". Error bars show 1 standard error of the mean.

The ANOVA revealed a significant main effect of DGd [$F(2, 42)=3.664$, $p=.034$; see Fig. 2], implicating that gaze behavior was evaluated differently with respect to the gaze duration. As Mauchly's test indicated that the assumption of the sphericity was fulfilled, no corrections of the degrees of freedom have been done. Trend analysis revealed a significant linear trend for gaze duration [$F(1, 21)=5.842$, $p=.025$], while pair-wise comparisons showed that the subjects' ratings were significantly different only between DG1 and DG4 (DG1 vs. DG4: $p=.025$; DG1 vs. DG2.5: $p=.105$; DG2.5 vs. DG4: $p=.287$). However, the difference between DG1 and DG4 did not survive the Bonferroni correction for multiple comparisons (DG1 vs. DG4: $p_c=.074$; DG1 vs. DG2.5: $p_c=.314$; DG2.5 vs. DG4: $p_c=.861$).

Neuroimaging results

Neural correlates of direct gaze

First, we directly compared DG and AG, thereby disregarding the variations in the duration of direct gaze. Consistent with earlier research, the contrast DG>AG yielded bilateral activations in temporo-occipital regions including the pSTS and the motion sensitive area (V5/MT+; see Fig. 3, left column and Table 1) (Malikovic et al., 2007), both areas frequently associated with gaze processing. The overlay of this contrast on a surface based representation of the MNI canonical brain using the SPM surfrend toolbox confirms that both bilateral activations extend into the pSTS (Fig. 3, left column). Furthermore, for the purpose of specific verification whether areas related to the main effect of the DG are affected by the duration of DG as well, we conducted the effect of DGd inclusively masked with the DG>AG contrast (mask threshold: $p<0.001$, uncorrected) without getting any significant results. Finally, the contrast AG>DG recruited the right middle occipital gyrus extending into the angular gyrus (see Table 1).

Neural correlates of direct gaze duration

Second, we tested for the first-order parametric modulation of direct gaze in order to identify regions where the activation increased linearly with an increasing duration of direct gaze. That is, we characterized brain areas in which higher activity was observed during prolonged direct gaze compared to shorter gaze duration. The

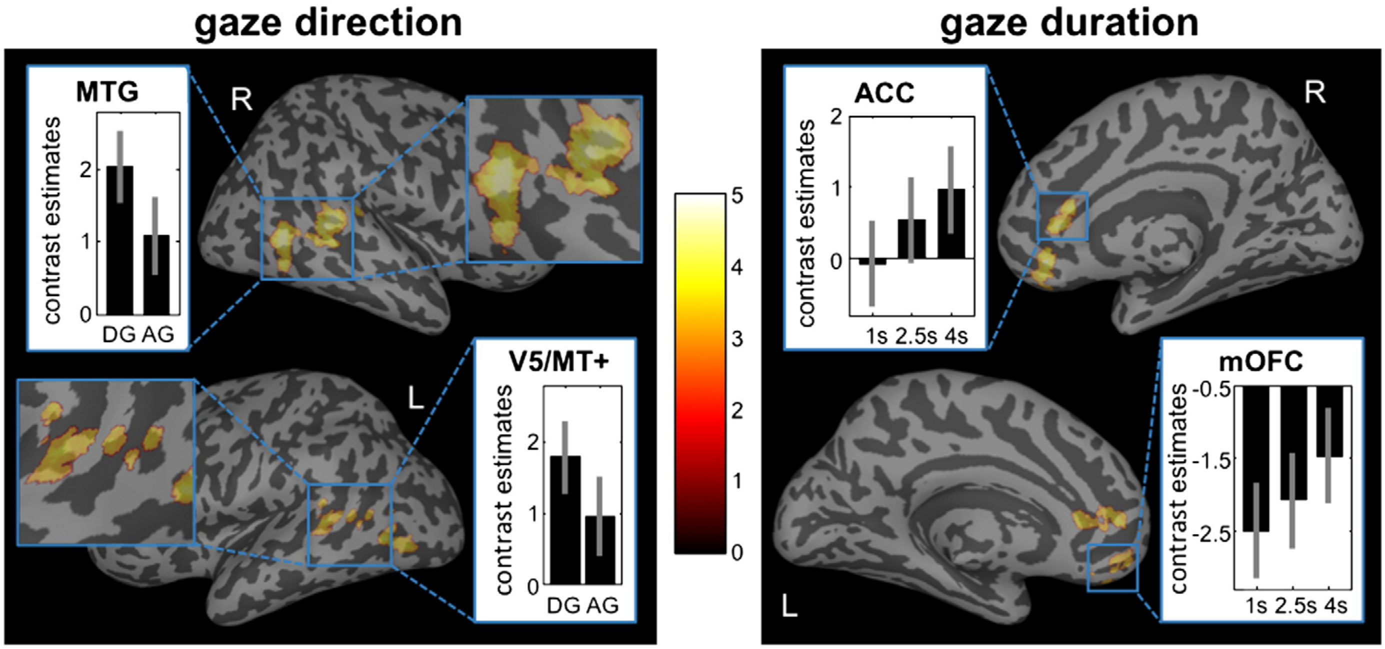

Fig. 3. Brain regions involved in the processing of gaze direction and gaze duration. The categorical comparison *direct gaze*>*averted gaze* yielded bilateral activations of the temporo-occipital regions including the posterior superior temporal sulcus and the V5/MT+ (left box). Plots illustrate the corresponding contrast estimates obtained for trials with direct gaze (DG) and trials with averted gaze (AG) for two different local maxima (upper plot: right MTG, $x=46$, $y=-44$, $z=9$; lower plot: left V5/MT+, $x=-42$, $y=-66$, $z=5$). On the other hand, parametric modulation analyses of fMRI data identified a region in the MPFC where BOLD signal changes increased linearly with the increasing *duration of the direct gaze* (right box). Plots illustrate corresponding contrast estimates obtained for trials with direct gaze at three levels of gaze duration (1 s, 2.5 s and 4 s) for two different local maxima (upper plot: supragenual ACC, $x=4$, $y=36$, $z=17$; lower plot: mOFC, $x=-4$, $y=48$, $z=-11$). The SPM{t} maps of these contrasts were overlaid on lateral and medial views of a surface based representation of the MNI canonical brain. The temporo-occipital regions were enlarged in order to demonstrate that activations extend into the pSTS. The bar in the middle represents the color coding of the *t*-values for overlaid SPM{t} maps. mOFC = medial orbitofrontal cortex, ACC = anterior cingulate cortex, MTG = middle temporal gyrus, V5/MT+ = motion sensitive area.

analysis showed that brain activity was modulated by DGd only in a single distributed area situated in the MPFC. The respective cluster of significant activation extended dorsally from the supragenual anterior cingulate cortex (ACC) into the pregenual ACC and the paracingulate cortex (PCC) and ventrally into the medial orbitofrontal cortex (mOFC; see Fig. 3, right column and Table 1). The differential activation of this cluster was characterized by deactivations relative to the resting baseline attenuating with increasing gaze duration, whereas only in the supragenual ACC (local maximum: $x=4$, $y=36$, $z=17$) changes in relative activations as a function of increasing gaze duration were detected (see Fig. 3, right column).

Additionally, in order to confirm the significant linear trend observed in the parametric modulation analysis, pair-wise comparisons of gaze duration conditions were performed in a supplementary random-effects analysis. The results showed that contrasting the longest with the shortest gaze duration (4 s>1 s) yielded activation of the MPFC (and additional areas, see Table 1), thus overlapping with the results from the parametric analysis. In parallel to behavior results, no other pair-wise comparisons reached significance.

Finally, in order to explore DGd-sensitive responses in additional, subcortical regions, a ROI analysis for the bilateral striatum was carried out. This analysis yielded no significant results, even when applying a liberal significance threshold ($p_c<0.1$, FWE-corrected).

Discussion

The main result of this study shows that processing gaze direction and gaze duration recruit distinct neural systems. Whereas the comparison of direct gaze with averted gaze, irrespective of gaze duration, yielded prominent activations in bilateral occipito-temporal regions including the pSTS as a correlate of socially relevant *gaze direction processing*, the *processing of gaze duration* was associated with differential neural activity in the MPFC.

Processing of gaze direction

The pSTS is well known to be involved in processing of various kinds of biological motion, including gaze movements in particular (Allison et al., 2000; Grossman and Blake, 2002; Pelphrey et al., 2003a, b; Puce et al., 1998). That is, the activation of the pSTS may in part be driven simply by the presence of eye gaze shifts as a form of biological motion in the DG (but not in the AG) condition. In addition to this concept of an “eye movement detector”, however, empirical evidence has also reliably indicated that pSTS activity shows context-dependent modulation of its response to gaze behavior. This suggests that the pSTS is also involved in the analysis of social information and intentions conveyed by gaze (Bristow et al., 2006; Hooker et al., 2003; Pelphrey et al., 2004a,b). In support of this notion, Pelphrey et al. (2004b) showed that the pSTS responded stronger to direct than averted gaze within an overt social context — even when both conditions contained the same movement quantity. While the present data may not differentiate between such contextual effects and biological motion driven activity, it must be assumed that both mechanisms coexist and constitute a dynamic hierarchical system for processing socially relevant stimuli.

The recruitment of V5/MT+ for the processing of the direct gaze direction might be evoked by the (physical) movement brought on by the eye gaze shifts in the DG condition, which was absent in the AG condition. Supporting this view, previous neuroimaging and neurophysiological studies have demonstrated the involvement of this region not only in processing of visual motion in general (Born and Bradley, 2005; Wilms et al., 2005) but also a specific effect of eye motion on the V5/MT+ activity (Puce et al., 1998; Watanabe et al., 2001, 2006).

Our results hence replicate previous findings on the involvement of the pSTS and V5/MT+ in gaze processing adding to the concept validity of our paradigm and the employed virtual characters.

Table 1
Brain areas involved in the processing of gaze direction and gaze duration.

Region	Cluster size	Cluster p_c	Side	x	y	z	T
Gaze direction							
DG>AG							
Middle temporal gyrus, extending to:	414	.000	R	46	−44	9	5.11
Superior temporal gyrus			R	58	−36	13	5.06
Middle temporal gyrus	251	.003	R	56	−66	−1	5.11
Middle occipital gyrus, extending to:	360	.000	L	−42	−66	5	4.16
Middle temporal gyrus			L	−48	−44	7	3.90
AG>DG							
Middle occipital gyrus, extending to:	203	.008	R	50	−76	27	4.60
Angular gyrus			R	48	−74	37	4.13
Gaze duration							
DGd							
mOFC, extending to:	640	.000	R	6	38	−11	4.77
			L	−4	48	−11	3.88
Supragenual ACC			R	4	36	17	4.37
Pregenual ACC			*R*	*6*	*38*	*5*	*4.24*
PCC			L	−10	50	5	3.97
4 s>1 s							
Pregenual ACC, extending to:	718	.000	R	8	36	5	5.20
			L	−2	36	5	4.71
mOFC			R	6	38	−11	4.42
			L	−4	46	−13	4.14
Insula	386	.000	L	−36	0	−1	4.81
Middle temporal gyrus	204	.008	L	−62	−46	−7	5.47
Inferior frontal gyrus	199	.009	R	50	28	−9	4.40

Comments underneath the table: Included are (i) results of the random-effects analysis testing for categorical differences between direct (DG) and averted (AG) gaze direction and computing the linear parametric modulation of neural responses to direct gaze by corresponding gaze durations (DGd); as well as (ii) results of supplementary random-effects analysis yielding significant results for the pair-wise comparison between the longest (4 s) and the shortest (1 s) direct gaze duration (4 s>1 s). *x*, *y* and *z* refer to the MNI stereotactic coordinates. R = right hemisphere, L = left hemisphere, mOFC = medial orbitofrontal cortex, ACC = anterior cingulate cortex, PCC = paracingulate cortex. For each presented cluster, coordinates at the maximum voxel are reported in the same row as the cluster size. Within extended clusters, coordinates for additional local maxima are indicated in rows below the respective cluster size declaration.

Moreover, these findings confirm the current hypothesis, that the combination of activation in the pSTS with one in V5/MT+ is highly important for processing the dynamic aspects of facial and in particular gaze stimuli (Johnson and Farroni, 2007). However, neural correlates of the simple comparison between the direct and the averted gaze are clearly restricted to posterior occipito-temporal areas thereby sparing any differential activation of medial frontal cortical regions. At the same time, changes in DGd did not differentially activate brain regions responsive to gaze direction, corroborated by the lack of significant results for the effect of DGd inclusively masked by the DG>AG contrast. In other words, the elicited activations in these areas were comparable in magnitude for all direct gaze conditions indicating that the modulating effect of varying *DGd* does not relate to sensory decoding, but relies on more complex cognitive processes as indicated by the MPFC activation.

Processing of gaze duration

In order to expand previous work on gaze perception, we focused our experimental design and analysis also on the question, to which extent the neural processing of direct gaze might be modulated by its temporal characteristics, i.e., duration of direct gaze. In accordance with prior behavioral data (Argyle et al., 1974; Brooks et al., 1986; Droney and Brooks, 1993; Gueguen and Jacob, 2002; Knackstedt and Kleinke, 1991), likeability ratings of stimulus faces increased with increasing gaze duration indicating the overall positive effect of prolonged gaze on impression formation. The corresponding neuroimaging data demonstrated that a positive correlation of signal increases with increasing gaze duration was present in the MPFC including the supragenual and pregenual ACC, the PCC as well as the mOFC. The modulatory effect of DGd on the activity in the MPFC was additionally validated by overlapping results of the direct comparison between the longest and the shortest gaze duration (4 s>1 s).

Within this DGd-responsive MPFC cluster, the PCC represents a specific functional division. Converging evidence from neuroimaging studies has demonstrated that the PCC is consistently recruited in the context of tasks requiring person judgments, self-referential processing and mentalizing (Amodio and Frith, 2006; Mitchell et al., 2005; Zysset et al., 2002). For instance, similar MPFC regions have been implicated in understanding communicative, interactively relevant intentions of others (Walter et al., 2004). Given that the duration of the direct gaze informs us about other persons' mental states (Eskritt and Lee, 2007), reflections on possible intentions of the displayed characters for the purpose of interpreting the “meaning” behind the gaze behavior might have been involved in the process of person perception in our study. Thus, the particular experience of increasing salience and communicational content of prolonged direct gaze might have resulted in differential amounts of spontaneous mentalizing processes that are not identifiable when gaze duration is disregarded. Furthermore, as direct gaze displayed by another person serves as an indicator of a potential social interaction and initiates social attention (Kampe et al., 2003; Kleinke, 1986; Mirenda et al., 1983; von Grunau and Anston, 1995), self-referential processing might have increased as a function of enhanced interpersonal involvement due to increasing direct gaze duration. In conclusion, the modulations of the PCC reported here might reflect a stronger engagement of meta-cognitive processes such as mentalizing and self-referential processing due to the manifest communicative intention of prolonged direct gaze.

In contrast to the PCC, the human mOFC plays a special role in representing the affective value of reinforcements thus enabling effective decision making and outcome monitoring as demonstrated both by neuroimaging (Amodio and Frith, 2006; Kringelbach, 2005; Kringelbach and Rolls, 2004) and lesion studies (Kringelbach and Rolls, 2004; Mah et al., 2004). Specifically face-evoked activation in the mOFC has been found to increase with increasing positive facial valence (Aharon et al., 2001; Kim et al., 2007; Kranz and Ishai, 2006;

O'Doherty et al., 2003). In these studies the valence of faces was dependent on different factors such as beauty (Aharon et al., 2001), the match between gender of the stimulus face and the sexual preference of the beholder (Kranz & Ishai, 2006), but also the display of a smile (O'Doherty et al., 2003). These data give rise to the suggestion that both morphological as well as dynamic self-referential nonverbal facial features can be considered as a reward similar to other primary and secondary reinforcements. Furthermore, evidence for the reward potential of direct gaze is already manifest in early ontogeny as even very young infants preferentially attend to faces with direct as compared to averted gaze (Farroni et al., 2002; Symons et al., 1998), show increased social smiling towards them (Hains and Muir, 1996) and improve affect regulation and suckling behaviour when experiencing direct gaze (Blass et al., 2007). Along the same line, eye contact has been found to serve as a reward in operant conditioning (Argyle and Cook, 1976). Accordingly, our results show an increase in neural activity in the mOFC corresponding to a higher degree of likeability with increasing duration of direct gaze. This finding supports the interpretation of the proposed reward that is associated with the prolonged direct gaze. As we controlled for attractiveness and emotional expression of the virtual characters, these factors can be excluded as potentially confounding variables.

However, the hypothesis of the increasing reward value of a prolonged direct gaze could not be substantiated further by ROI analyses focusing on striatal regions associated with reward processing. The lack of the involvement of striatal regions might be explained by dissociable roles of OFC and ventral striatum. The engagement of the mOFC was related to representation of the abstract and changing reward value of stimuli (Kringelbach and Rolls, 2004) and was maintained also when facial stimuli were repeatedly presented (Kim et al., 2007), like in the present paradigm. In contrast, the ventral striatum exhibited novelty-dependent and short-lasting involvement in facial preference decisions (Kim et al., 2007) probably being less suitable for monitoring meaningful changes in subtle nonverbal social expressions.

Nevertheless, the assumed reward effect of gaze duration due to the differential involvement of mOFC in response to increasing DGd needs to be handled with caution. Alternatively, the differential involvement of the mOFC can be related to general enhanced emotional processing in the context of the direct gaze as suggested by Conty et al. (2007) as well as by Wicker et al. (2003). Affirmatively, the DGd-responsive supragenual ACC has been frequently implicated in assessing emotional valence of internal and external stimuli (Bush et al., 2000; Devinsky et al., 1995). Moreover, extensive connections between the dorsal ACC and limbic regions including the mOFC, showing a differential response to varying DGd as well, have been described (Devinsky et al., 1995). Confirming the functional link between these two areas (Kringelbach and Rolls, 2004), dramatic behavioral changes have been reported to occur after combined lesions of the dorsal ACC and the mOFC leading to impaired ability to interpret social cues and to show physiological reactions to emotionally significant stimuli (Devinsky et al., 1995). Thus, as it could be demonstrated that being looked at comprises an emotional valence by heightening arousal (Argyle and Cook, 1976; Nichols and Champness, 1971; Wicker et al., 1998), the increasing activation of the supragenual ACC and the mOFC in response to increasing DGd might be induced by the affective content of a maintained, interpersonally involving direct gaze.

Finally, it should be emphasized that the gaze duration processing in the mOFC and the rostral MPFC including the pregenual ACC and the PCC pertained to the attenuation of deactivation relative to resting baseline whereas true activations were present only in the supragenual ACC. Signal decreases in medial prefrontal regions have been commonly observed during various attention-demanding cognitive tasks in functional imaging studies, including those focusing on emotional and non-emotional judgment of visual stimuli, while signal increases in these regions were present during resting states (Gusnard et al., 2001a; Heinzel et al., 2005; Northoff et al., 2004; Raichle et al., 2001; Schilbach et al., 2008). Taking this into account, the explicit instruction to evaluate stimulus faces used in our study may have induced goal-directed and externally oriented processing in the period of stimulus presentation and in turn resulted in a deactivation of the mOFC and the rostral MPFC when gaze duration effects are not considered. In this context, it is interesting to note that it has been speculated that the resting state is phenomenologically dominated by internally directed thoughts and social cognitive processes (Gusnard et al., 2001a,b; Iacoboni et al., 2004; Schilbach et al., 2008), as supported by self-reports of subjects at rest (D'Argembeau et al., 2005; Mazoyer et al., 2001) as well as by functional imaging studies (Iacoboni et al., 2004; Mitchell et al., 2005). Hence, gaze duration-dependent attenuation of signal decreases in these areas might reflect an increase of internal, socio-emotional processing induced by prolonged direct gaze.

Conclusions

In summary, cognitive processing of social gaze appears to be dependent on specific gaze parameters that have to be considered in detail. On the one hand, the *detection* of socially relevant *gaze direction* conveying the impression of being looked at by a virtual character, irrespective of gaze duration, appears to be mediated by bilateral occipito-temporal regions including the multimodal sensory area pSTS. Indicating social perception via complex visual analysis, the recruitment of these posterior brain regions may be related to the observation of incoming social stimuli. On the other hand, the involvement of the MPFC known to be involved in a variety of metacognitive processes suggests more complex processing related to the *evaluation* of the ongoing communicational input conveyed by the direct *gaze duration*. Within dynamic, stochastic environments like social encounters changing nonverbal signals including gaze behavior require sophisticated dynamic decoding of the underlying meaning that may provide an essential basis for the regulation of one's own actions and reactions. For online monitoring of the direct gaze duration that encloses a significant source of social information we demonstrated the engagement of PCC, ACC and mOFC traditionally associated with mentalizing on the one hand and with processing the hedonic and affective value of stimuli and possible outcomes on the other. Extending the perceptual detection of gaze direction, our results thus indicate that the systematic investigation of dynamic and subtle nonverbal signals such as direct gaze duration may help to better characterize the proposed link between direct gaze and complex social cognitive processes.

References

Aharon, I., Etcoff, N., Ariely, D., Chabris, C.F., O'Connor, E., Breiter, H.C., 2001. Beautiful faces have variable reward value: fMRI and behavioral evidence. Neuron 32, 537–551.

Akiyama, T., Kato, M., Muramatsu, T., Saito, F., Nakachi, R., Kashima, H., 2006. A deficit in discriminating gaze direction in a case with right superior temporal gyrus lesion. Neuropsychologia 44, 161–170.

Allison, T., Puce, A., McCarthy, G., 2000. Social perception from visual cues: role of the STS region. Trends Cogn. Sci. 4, 267–278.

Amodio, D.M., Frith, C.D., 2006. Meeting of minds: the medial frontal cortex and social cognition. Nat. Rev. Neurosci. 7, 268–277.

Argyle, M., Cook, M., 1976. Gaze and Mutual Gaze. Cambridge University Press, Cambridge.

Argyle, M., Dean, J., 1965. Eye-contact, distance and affiliation. Sociometry 28, 289–304.

Argyle, M., Lefebvre, L., Cook, M., 1974. The meaning of five patterns of gaze. Eur. J. Soc. Psychol. 4, 125–136.

Ashburner, J., Friston, K.J., 2003. Rigid body registration. In: Frackowiak, R.S., Friston, K.J., Frith, C.D., Dolan, R.J., Price, C.J., Ashburner, J., Penny, W.D., Zeki, S. (Eds.), Human Brain Function. Academic Press, San Diego; London, pp. 635–655.

Bailenson, J.N., Blascovich, J., Beall, A.C., Loomis, J.M., 2003. Interpersonal distance in immersive virtual environments. Pers. Soc. Psychol. Bull. 29, 819–833.

Baron-Cohen, S., 1995. Mindblindness: An Essay on Autism and Theory Of Mind. MIT Press, Cambridge, Mass.; London.

Bente, G., 1989. Facilities for the graphical computer simulation of head and body movements. Behav. Res. Meth. Instrum. Comput. 21, 455–462.

Bente, G., Feist, A., Elder, S., 1996. Person perception effects of computer-simulated male and female head movement/Personwahrnehmungseffekte von computersimulierten männlichen und weiblichen Kopfbewegungen. J. Nonverbal Behav. 20, 213–228.

Bente, G., Kraemer, N.C., Petersen, A., de Ruiter, J.P., 2001a. Computer animated movement and person perception: methodological advances in nonverbal behavior research. J. Nonverbal Behav. 25, 151–166.

Bente, G., Petersen, A., Kraemer, N.C., de Ruiter, J.P., 2001b. Transcript-based computer animation of movement: evaluating a new tool for nonverbal behavior research. Behav. Res. Meth. Instrum. Comput. 33, 303–310.

Blascovich, J., Loomis, J.M., Beall, A.C., Swinth, K.R., Hoyt, C.L., Bailenson, J.N., 2002. Immersive virtual environment technology as a methodological tool for social psychology. Psychol. Inq. 13, 103–124.

Blass, E.M., Lumeng, J., Patil, N., 2007. Influence of mutual gaze on human infant affect. In: Flom, R., Lee, K., Muir, D. (Eds.), Gaze-following: Its Development and Significance. Lawrence Erlbaum Associates, Mahwah, N.J.; London, pp. 113–143.

Born, R.T., Bradley, D.C., 2005. Structure and function of visual area MT. Annu. Rev. Neurosci. 28, 157–189.

Bristow, D., Rees, G., Frith, C.D., 2006. Social interaction modifies neural response to gaze shifts. Soc. Cognitive Affect. Neurosci. 2, 52–61.

Brooks, C.I., Church, M., A, Fraser, L., 1986. Effects of duration of eye contact on judgments of personality characteristics. J. Soc. Psychol. 126, 71–78.

Bush, G., Luu, P., Posner, M.I., 2000. Cognitive and emotional influences in anterior cingulate cortex. Trends Cogn. Sci. 4, 215–222.

Calder, A.J., Lawrence, A.D., Keane, J., Scott, S.K., Owen, A.M., Christoffels, I., Young, A.W., 2002. Reading the mind from eye gaze. Neuropsychologia 40, 1129–1138.

Collins, D.L., Neelin, P., Peters, T.M., Evans, A.C., 1994. Automatic 3D intersubject registration of MR volumetric data in standardized Talairach space. J. Comput. Assist. Tomogr. 18, 192–205.

Conty, L., N'Diaye, K., Tijus, C., George, N., 2007. When eye creates the contact! ERP evidence for early dissociation between direct and averted gaze motion processing. Neuropsychologia 45, 3024–3037.

D'Argembeau, A., Collette, F., Van der Linden, M., Laureys, S., Del Fiore, G., Degueldre, C., Luxen, A., Salmon, E., 2005. Self-referential reflective activity and its relationship with rest: a PET study. Neuroimage 25, 616–624.

Dale, A.M., 1999. Optimal experimental design for event-related fMRI. Hum. Brain Mapp. 8, 109–114.

Devinsky, O., Morrell, M.J., Vogt, B.A., 1995. Contributions of anterior cingulate cortex to behaviour. Brain 118 (Pt 1), 279–306.

Droney, J.M., Brooks, C.I., 1993. Attributions of self-esteem as a function of duration of eye contact. J. Soc. Psychol. 133, 715–722.

Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., Zilles, K., 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. Neuroimage 25, 1325–1335.

Eickhoff, S.B., Heim, S., Zilles, K., Amunts, K., 2006. Testing anatomically specified hypotheses in functional imaging using cytoarchitectonic maps. Neuroimage 32, 570–582.

Eickhoff, S.B., Paus, T., Caspers, S., Grosbras, M.H., Evans, A.C., Zilles, K., Amunts, K., 2007. Assignment of functional activations to probabilistic cytoarchitectonic areas revisited. Neuroimage 36, 511–521.

Einav, S., Hood, B.M., 2006. Children's use of the temporal dimension of gaze for inferring preference. Dev. Psychol. 42, 142–152.

Eskritt, M., Lee, K., 2007. Preschoolers' use of eye gaze for "mind reading". In: Flom, R., Lee, K., Muir, D. (Eds.), Gaze-following: Its Development and Significance. Lawrence Erlbaum Associates, Mahwah, N.J.; London, pp. 243–263.

Evans, A.C., Marrett, S., Neelin, P., Collins, L., Worsley, K., Dai, W., Milot, S., Meyer, E., Bub, D., 1992. Anatomical mapping of functional activation in stereotactic coordinate space. Neuroimage 1, 43–53.

Farroni, T., Csibra, G., Simion, F., Johnson, M.H., 2002. Eye contact detection in humans from birth. Proc. Natl. Acad. Sci. U. S. A. 99, 9602–9605.

Friston, K.J., Holmes, A., Poline, J.B., Price, C.J., Frith, C.D., 1996. Detecting activations in PET and fMRI: levels of inference and power. Neuroimage 4, 223–235.

Frith, U., 2001. Mind blindness and the brain in autism. Neuron 32, 969–979.

Gallagher, H.L., Jack, A.I., Roepstorff, A., Frith, C.D., 2002. Imaging the intentional stance in a competitive game. Neuroimage 16, 814–821.

George, N., Driver, J., Dolan, R.J., 2001. Seen gaze-direction modulates fusiform activity and its coupling with other brain areas during face processing. Neuroimage 13, 1102–1112.

Gibson, J.J., Pick, A.D., 1963. Perception of another person's looking behavior. Am. J. Psychol. 76, 386–394.

Gobbini, M.I., Koralek, A.C., Bryan, R.E., Montgomery, K.J., Haxby, J.V., 2007. Two takes on the social brain: a comparison of theory of mind tasks. J. Cogn. Neurosci. 19, 1803–1814.

Gopnik, A., Slaughter, V., Meltzoff, A., 1994. Changing your views: how understanding visual perception can lead to a new theory of mind. In: Lewis, C., Mitchell, P. (Eds.), Children's Early Understanding Of Mind. Lawrence Erlbaum Associates, UK, pp. 157–183.

Grossman, E.D., Blake, R., 2002. Brain areas active during visual perception of biological motion. Neuron 35, 1167–1175.

Gueguen, N., Jacob, C., 2002. Direct look versus evasive glance and compliance with a request. J. Soc. Psychol. 142, 393–396.

Gusnard, D.A., Akbudak, E., Shulman, G.L., Raichle, M.E., 2001a. Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. Proc. Natl. Acad. Sci. U. S. A. 98, 4259–4264.

Gusnard, D.A., Raichle, M.E., Raichle, M.E., 2001b. Searching for a baseline: functional imaging and the resting human brain. Nat. Rev. Neurosci. 2, 685–694.

Hains, S.M., Muir, D.W., 1996. Infant sensitivity to adult eye direction. Child Dev. 67, 1940–1951.

Heinzel, A., Bermpohl, F., Niese, R., Pfennig, A., Pascual-Leone, A., Schlaug, G., Northoff, G., 2005. How do we modulate our emotions? Parametric fMRI reveals cortical midline structures as regions specifically involved in the processing of emotional valences. Brain Res. Cogn. Brain Res. 25, 348–358.

Hoffman, E.A., Haxby, J.V., 2000. Distinct representations of eye gaze and identity in the distributed human neural system for face perception. Nat. Neurosci. 3, 80–84.

Holmes, C.J., Hoge, R., Collins, L., Woods, R., Toga, A.W., Evans, A.C., 1998. Enhancement of MR images using registration for signal averaging. J. Comput. Assist. Tomogr. 22, 324–333.

Hood, B.M., Macrae, C.N., 2007. Look into my eyes: the effect of direct gaze on face processing in children and adults. In: Flom, R., Lee, K., Muir, D. (Eds.), Gaze-following: Its Development and Significance. Lawrence Erlbaum Associates, Mahwah, N.J.; London, pp. 297–383.

Hooker, C.I., Paller, K.A., Gitelman, D.R., Parrish, T.B., Mesulam, M.M., Reber, P.J., 2003. Brain networks for analyzing eye gaze. Brain Res. Cogn. Brain Res. 17, 406–418.

Iacoboni, M., Lieberman, M.D., Knowlton, B.J., Molnar-Szakacs, I., Moritz, M., Throop, C.J., Fiske, A.P., 2004. Watching social interactions produces dorsomedial prefrontal and medial parietal BOLD fMRI signal increases compared to a resting baseline. Neuroimage 21, 1167–1173.

Johnson, M.H., Farroni, T., 2007. The neurodevelopmental origins of eye gaze perception. In: Flom, R., Lee, K., Muir, D. (Eds.), Gaze-following: Its Development and Significance. Lawrence Erlbaum Associates, Mahwah, N.J.; London, pp. 1–17.

Kampe, K.K., Frith, C.D., Frith, U., 2003. "Hey John": signals conveying communicative intention toward the self activate brain regions associated with "mentalizing", regardless of modality. J. Neurosci. 23, 5258–5263.

Kawashima, R., Sugiura, M., Kato, T., Nakamura, A., Hatano, K., Ito, K., Fukuda, H., Kojima, S., Nakamura, K., 1999. The human amygdala plays an important role in gaze monitoring. A PET study. Brain 122 (Pt 4), 779–783.

Kim, H., Adolphs, R., O'Doherty, J.P., Shimojo, S., 2007. Temporal isolation of neural processes underlying face preference decisions. Proc. Natl. Acad. Sci. U. S. A. 104, 18253–18258.

Kleinke, C.L., 1986. Gaze and eye contact: a research review. Psychol. Bull. 100, 78–100.

Knackstedt, G., Kleinke, C.L., 1991. Eye contact, gender, and personality judgments. J. Soc. Psychol. 131, 303–304.

Kranz, F., Ishai, A., 2006. Face perception is modulated by sexual preference. Curr. Biol. 16, 63–68.

Kringelbach, M.L., 2005. The human orbitofrontal cortex: linking reward to hedonic experience. Nat. Rev., Neurosci. 6, 691–702.

Kringelbach, M.L., Rolls, E.T., 2004. The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. Prog. Neurobiol. 72, 341–372.

Ku, J., Jang, H.J., Kim, K.U., Kim, J.H., Park, S.H., Lee, J.H., Kim, J.J., Kim, I.Y., Kim, S.I., 2005. Experimental results of affective valence and arousal to avatar's facial expressions. Cyberpsychol. Behav. 8, 493–503.

Lancaster, J.L., Woldorff, M.G., Parsons, L.M., Liotti, M., Freitas, C.S., Rainey, L., Kochunov, P.V., Nickerson, D., Mikiten, S.A., Fox, P.T., 2000. Automated Talairach atlas labels for functional brain mapping. Hum. Brain Mapp. 10, 120–131.

Liu, X., Powell, D.K., Wang, H., Gold, B.T., Corbly, C.R., Joseph, J.E., 2007. Functional dissociation in frontal and striatal areas for processing of positive and negative reward information. J. Neurosci. 27, 4587–4597.

Mah, L., Arnold, M.C., Grafman, J., 2004. Lesions of prefrontal cortex impair social perception. Am. J. Psychiatr. 161, 1247–1255.

Maldjian, J.A., Laurienti, P.J., Kraft, R.A., Burdette, J.H., 2003. An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. Neuroimage 19, 1233–1239.

Malikovic, A., Amunts, K., Schleicher, A., Mohlberg, H., Eickhoff, S.B., Wilms, M., Palomero-Gallagher, N., Armstrong, E., Zilles, K., 2007. Cytoarchitectonic analysis of the human extrastriate cortex in the region of V5/MT+: a probabilistic, stereotaxic map of area hOc5. Cereb. Cortex 17, 562–574.

Mason, M.F., Tatkow, E.P., Macrae, C.N., 2005. The look of love: gaze shifts and person perception. Psychol. Sci. 16, 236–239.

Mazoyer, B., Zago, L., Mellet, E., Bricogne, S., Etard, O., Houde, O., Crivello, F., Joliot, M., Petit, L., Tzourio-Mazoyer, N., 2001. Cortical networks for working memory and executive functions sustain the conscious resting state in man. Brain Res. Bull. 54, 287–298.

Mirenda, P.L., Donnellan, A.M., Yoder, D.E., 1983. Gaze behavior: a new look at an old problem. J. Autism. Dev. Disord. 13, 397–409.

Mitchell, J.P., Banaji, M.R., Macrae, C.N., 2005. The link between social cognition and self-referential thought in the medial prefrontal cortex. J. Cogn. Neurosci. 17, 1306–1315.

Montgomery, D.E., Bach, L.M., Moran, C., 1998. Children's use of looking behavior as a cue to detect another's goal. Child Dev. 69, 692–705.

Moser, E., Derntl, B., Robinson, S., Fink, B., Gur, R.C., Grammer, K., 2007. Amygdala activation at 3 T in response to human and avatar facial expressions of emotions. J. Neurosci. Methods 161, 126–133.

Nichols, K.A., Champness, B.G., 1971. Eye gaze and the GSR. J. Exp. Soc. Psychol. 7, 623–626.

Northoff, G., Heinzel, A., Bermpohl, F., Niese, R., Pfennig, A., Pascual-Leone, A., Schlaug, G., 2004. Reciprocal modulation and attenuation in the prefrontal cortex: an fMRI study on emotional–cognitive interaction. Hum. Brain Mapp. 21, 202–212.

O'Doherty, J.P., 2004. Reward representations and reward-related learning in the human brain: insights from neuroimaging. Curr. Opin. Neurobiol. 14, 769–776.

O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D.M., Dolan, R.J., 2003. Beauty in a smile: the role of medial orbitofrontal cortex in facial attractiveness. Neuropsychologia 41, 147–155.

Ochsner, K.N., Beer, J.S., Robertson, E.R., Cooper, J.C., Gabrieli, J.D., Kihsltrom, J.F., D'Esposito, M., 2005. The neural correlates of direct and reflected self-knowledge. Neuroimage 28, 797–814.

Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9, 97–113.

Omori, Y., Miyata, Y., 2001. Estimates of impressions based on frequency of blinking. Soc. Behav. Personal. 29, 159–168.

Pelphrey, K.A., Mitchell, T.V., McKeown, M.J., Goldstein, J., Allison, T., McCarthy, G., 2003a. Brain activity evoked by the perception of human walking: controlling for meaningful coherent motion. J. Neurosci. 23, 6819–6825.

Pelphrey, K.A., Singerman, J.D., Allison, T., McCarthy, G., 2003b. Brain activation evoked by perception of gaze shifts: the influence of context. Neuropsychologia 41, 156–170.

Pelphrey, K.A., Morris, J.P., McCarthy, G., 2004a. Grasping the intentions of others: the perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. J. Cogn. Neurosci. 16, 1706–1716.

Pelphrey, K.A., Viola, R.J., McCarthy, G., 2004b. When strangers pass: processing of mutual and averted social gaze in the superior temporal sulcus. Psychol Sci 15, 598–603.

Penny, W.D., Holmes, A.P., 2003. Random effects analysis. In: Frackowiak, R.S., Friston, K.J., Frith, C.D., Dolan, R.J., Price, C.J., Ashburner, J., Penny, W.D., Zeki, S. (Eds.), Human Brain Function. Academic Press, San Diego; London, pp. 843–850.

Premack, D., Woodruff, G., 1978. Does the chimpanzee have a theory of mind? Behav. Brain Sci. 1, 515–526.

Puce, A., Allison, T., Bentin, S., Gore, J.C., McCarthy, G., 1998. Temporal cortex activation in humans viewing eye and mouth movements. J. Neurosci. 18, 2188–2199.

Raichle, M.E., MacLeod, A.M., Snyder, A.Z., Powers, W.J., Gusnard, D.A., Shulman, G.L., 2001. A default mode of brain function. Proc. Natl. Acad. Sci. U. S. A. 98, 676–682.

Schilbach, L., Wohlschlaeger, A.M., Kraemer, N.C., Newen, A., Shah, N.J., Fink, G.R., Vogeley, K., 2006. Being with virtual others: neural correlates of social interaction. Neuropsychologia 44, 718–730.

Schilbach, L., Eickhoff, S.B., Rotarska-Jagiela, A., Fink, G.R., Vogeley, K., 2008. Minds at rest? Social cognition as the default mode of cognizing and its putative relationship to the “default system” of the brain. Conscious. Cogn. 17, 457–467.

Serences, J.T., 2004. A comparison of methods for characterizing the event-related BOLD timeseries in rapid fMRI. Neuroimage 21, 1690–1700.

Symons, L.A., Hains, S.M.J., Muir, D.W., 1998. Look at me: five-month-old infants' sensitivity to very small deviations in eye-gaze during social interactions. Infant Behavi. Dev. 21, 531–536.

Valentine, M.E., Ehrlichman, H., 1979. Interpersonal gaze and helping behavior. J. Soc. Psychol. 107, 193–198.

Vogeley, K., Bussfeld, P., Newen, A., Herrmann, S., Happe, F., Falkai, P., Maier, W., Shah, N.J., Fink, G.R., Zilles, K., 2001. Mind reading: neural mechanisms of theory of mind and self-perspective. Neuroimage 14, 170–181.

von Grunau, M., Anston, C., 1995. The detection of gaze direction: a stare-in-the-crowd effect. Perception 24, 1297–1313.

Vuilleumier, P., Pourtois, G., 2007. Distributed and interactive brain mechanisms during emotion face perception: evidence from functional neuroimaging. Neuropsychologia 45, 174–194.

Vuilleumier, P., George, N., Lister, V., Armony, J., Driver, J., 2005. Effects of perceived mutual gaze and gender on face processing and recognition memory. Vis. Cogn. 12, 85–101.

Walter, H., Adenzato, M., Ciaramidaro, A., Enrici, I., Pia, L., Bara, B.G., 2004. Understanding intentions in social interaction: the role of the anterior paracingulate cortex. J. Cogn. Neurosci. 16, 1854–1863.

Watanabe, S., Kakigi, R., Puce, A., 2001. Occipitotemporal activity elicited by viewing eye movements: a magnetoencephalographic study. Neuroimage 13, 351–363.

Watanabe, S., Kakigi, R., Miki, K., Puce, A., 2006. Human MT/V5 activity on viewing eye gaze changes in others: a magnetoencephalographic study. Brain Res. 1092, 152–160.

Wicker, B., Michel, F., Henaff, M.A., Decety, J., 1998. Brain regions involved in the perception of gaze: a PET study. Neuroimage 8, 221–227.

Wicker, B., Perrett, D.I., Baron-Cohen, S., Decety, J., 2003. Being the target of another's emotion: a PET study. Neuropsychologia 41, 139–146.

Wilms, M., Eickhoff, S.B., Specht, K., Amunts, K., Shah, N.J., Malikovic, A., Fink, G.R., 2005. Human V5/MT+: comparison of functional and cytoarchitectonic data. Anat. Embryol. (Berl) 210, 485–495.

Zysset, S., Huber, O., Ferstl, E., von Cramon, D.Y., 2002. The anterior frontomedian cortex and evaluative judgment: an fMRI study. Neuroimage 15, 983–991.

Research in Autism Spectrum Disorders 5 (2011) 604–613

Contents lists available at ScienceDirect

Research in Autism Spectrum Disorders

Journal homepage: http://ees.elsevier.com/RASD/default.asp

A matter of words: Impact of verbal and nonverbal information on impression formation in high-functioning autism

Bojana Kuzmanovic [a,*], Leonhard Schilbach [a], Fritz-Georg Lehnhardt [a], Gary Bente [b], Kai Vogeley [a]

[a] Department of Psychiatry and Psychotherapy, University Hospital Cologne, Germany
[b] Department of Psychology, University of Cologne, Germany

ARTICLE INFO

Article history:
Received 27 May 2010
Accepted 16 July 2010

Keywords:
Impression formation
High-functioning autism
Verbal
Nonverbal

ABSTRACT

Clinical intuition and resent research (Senju et al., 2009) suggests that adults with high-functioning autism (HFA) are able to use explicit verbal information but fail to react upon subtle nonverbal cues in order to understand others and navigate social encounters.

In order to investigate the relative influence of different domains of socially relevant information in HFA as compared to matched controls, we used verbal and nonverbal stimuli as a basis for an interpersonal impression formation task. Results demonstrated a reduced sensitivity to nonverbal cues in individuals with HFA when consideration of conflicting information from the different domains was required, although HFA participants could well evaluate nonverbal stimuli in isolation. Thus, in a more complex experimental setting nonverbal information had a comparably weak impact on the impression formation confirming that social processing is preferentially based on verbal information in HFA.

1. Introduction

Research on the ability to understand mental states of others, also referred to as 'theory of mind' (ToM), has been highly influential in characterizing social cognition in individuals with autism (Frith, 2003). Here, impairments in ToM abilities helped to explain core criteria of autism including qualitative impairments in social communication and reciprocal interaction (10th revision of the International Classification of Diseases, ICD-10, World Health Organization). However, in everyday social interactions, we do not only reason about the mental states of others in a given situation – as tested in 'classical' ToM tasks – but we also form global evaluative impressions of others, i.e., we feel more or less attracted by the other person. These first impressions not only play a substantial role in interpersonal decision-making with respect to private relationships, but also in professional contexts, mass media or politics (Frey, 1999).

Recent dual-processing accounts of judgment and social cognition assume that (i) the verbal descriptions of the behavior of others (propositional format) and (ii) visual observation of nonverbal behavior (non-propositional format) have different processing paths (Evans, 2008): while nonverbal behavior of others has been demonstrated to play an influential role in the impression formation process (Burgoon, 1994; Domangue, 1978; Droney & Brooks, 1993; Kuzmanovic et al., 2009; Levine & Feldman, 2002; Scherer, Scherer, Hall, & Rosenthal, 1977), it does not necessarily refer to an explicit semantic code like the symbolic verbal information making it on occasion difficult to extract a distinct declarative meaning from single cues (Bente

---

* Corresponding author at: Department of Psychiatry and Psychotherapy, University Hospital Cologne, Kerpener Str. 62, 50924 Cologne, Germany. Tel.: +49 221 478 87141.
E-mail address: bojana.kuzmanovic@uk-koeln.de (B. Kuzmanovic).

1750-9467/$ – see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.rasd.2010.07.005

& Kraemer, 2003; Bente & Kraemer, 2008; Bente, Kraemer, & Eschenburg, 2008; Kraemer, 2008). Further characteristics of nonverbal behavior that add to the difficulty of its explicit interpretation are its (i) high *dimensional* complexity which refers to the simultaneous co-occurrence of multiple cues (e.g., smile and direct gaze) and the interdependency of meanings of the different cues on each other and (ii) the high *processual* complexity which denotes the quality of movements characterized by subtle dynamics extending in time rather than static, isolated elements (Bente & Kraemer, 2003, 2008; Bente, Kraemer, & Eschenburg, 2008; Grammer, Honda, Juette, & Schmitt, 1999; Kraemer, 2008). Consequently, nonverbal behavior is often produced and decoded outside awareness (Choi, Gray, & Ambady, 2005; Frey, 1999; Gilbert & Krull, 1988; Grammer et al., 1999) and thus might influence the impression formation in a more intuitive way.

Despite the importance of impression formation for social interaction and communication and in contrast to the numerous studies on ToM, there have been no attempts to investigate whether and how individuals with HFA form global evaluative impressions of other people. In the present study, we, therefore, devised an impression formation task that not only requires an understanding of current mental states of another person, but also demands an evaluative assessment of the target person based on verbal behavioral descriptions and nonverbal behavioral samples. In a complex impression formation task, verbal (V) and nonverbal (N) information was presented in a congruent (i.e., V+N+ or V−N−) or in an incongruent (i.e., V−N+ or V+N−) combination with respect to valence (positive +, or negative −). This design allowed for investigating the differential impacts of verbal and nonverbal components of information on the global person evaluation. Additionally, in order to acquire the subjective evaluations of each verbal and nonverbal stimulus for each participant all stimuli were also presented separately in a basic control task. In light of previous studies reporting processing differences for nonverbal social stimuli in HFA (Baron-Cohen et al., 1999; Behrmann et al., 2006; Critchley et al., 2000; Schultz et al., 2000), we expected HFA participants to exhibit difficulties in the decoding and consideration of dynamic, nonverbal cues rather than verbal information during impression formation, particularly during the complex incongruent task in which conflicting information had to be integrated to form a context-sensitive global impression of the other person.

2. Materials and methods

2.1. Participants

Fifteen HFA individuals (11 male, mean age 30.47, SD = 7.11 years) were studied and compared to 15 control participants (11 male, mean age 29.87, SD = 6.40 years) who were matched with respect to gender, age, years of education and intelligence (see Table 1). All HFA participants were diagnosed and recruited in the Autism Outpatient Clinic at the Department of Psychiatry at the University of Cologne (Germany). As part of a systematic assessment the diagnoses were made independently by two specialized physicians corresponding to ICD-10 criteria and were supplemented by an extensive neuropsychological assessment. The procedure of this assessment began with a first interview with patients by a specialized consulting physician (LS or FGL), who were referred to our department by a practicing psychiatrist or neurologist in order to confirm or reject the possible diagnosis of autism. In cases in which this first interview supported the diagnosis, patients underwent a neuropsychological assessment resulting in a detailed written summary of the neuropsychological profile including comments on the behavior of the patients during the testing. In a final interview with the patient, the decision was made by a second, independent consulting physician (KV) under considerations of the previous indices. Included were patients with the diagnoses childhood autism (F84.0) and Asperger's autism (F84.5) with an at least averaged IQ. Thus, we use the term HFA to refer to individuals with autism spectrum disorders and a high intellectual level of functioning regardless of diagnostic criteria relating to early childhood such as the onset of the language development. None of the HFA participants were taking any psychotropic medications except for one who was taking an antidepressant medication (Sertraline 50 mg/day). As depression is a common co-morbidity in HFA (Stewart, Barnard, Pearson, Hasan, & O'Brien, 2006) and this individual's neuropsychological performance was comparable to the rest of the group, he was not excluded.

Table 1
Demographic and neuropsychological variables.

	HFA		Control		Statistics	
	M	SD	*M*	SD		
Gender (m:f)	11:4		11:4			
Age (y)	30.47	7.11	29.87	6.40	$t(28) = .24$	$p = .81$
Education (y)	17.67	4.16	17.97	2.54	$t(28) = -.24$	$p = .81$
IQ	111.64	5.92	110.20	8.17	$t(28) = .36$	$p = .73$
BDI[a]	11.87	10.77	2.27	2.68	$t(28) = 3.35$	$p = .00^{*}$
AQ[a]	37.60	4.27	13.60	3.70	$t(28) = 16.45$	$p = .00^{*}$
EQ[a]	16.25	8.61	47.87	9.85	$t(25) = -8.75$	$p = .00^{*}$
SQ[a]	34.42	16.28	26.33	9.74	$t(25) = 1.60$	$p = .12$

HFA = high-functioning autism, *M* = mean, SD = standard deviation, m = male, f = female, y = years, BDI = Beck Depression Inventory, AQ = Autism Spectrum Quotient, EQ = Empathy Quotient, SQ = Systemizing Quotient-Revised.
Note: The EQ- and SQ-scores of three HFA participants are missing.

[a] Raw score (not standardized).

* $p < .05$.

Additionally, three people reported episodes of depression in their past medical history. Accordingly, there was a significant difference in the Beck Depression Inventory (BDI) (Beck & Steer, 1987) score for the control and the HFA group (see Table 1). Consistent with the clinical diagnoses, there were also significant differences in the Autism Spectrum Quotient (AQ) and the Empathy Quotient (EQ) as well as trend level significant differences in the Systemizing Quotient-Revised (SQ) between the HFA and the control group (see Table 1) (Wheelwright et al., 2006).

Controls were recruited online by addressing students and employees of the University of Cologne. They had no history of neurological or psychiatric disorders, and were not on any kind of psychotropic medication. Furthermore, they were only included if providing an average AQ (critical cut-off score ≤ 22) (Baron-Cohen, 2003) and a normal BDI score (Beck & Steer, 1987) in order to avoid extensive depressive or autistic symptoms in the healthy, control sample. Intelligence in both groups for matching purposes was assessed by a German multiple choice vocabulary test ("Wortschatztest", WST) (Schmidt & Metzler, 1992), which allows a quick and valid estimation of general intelligence (Lehrl, Triebig, & Fischer, 1995; Suslow, 2009). Participants gave their informed consent before taking part. The study was conducted with the approval of the local ethics committee of the Medical Faculty of the University of Cologne.

2.2. Stimuli

Verbal stimuli consisted of 12 positive (V+) and 12 negative (V−) German sentences describing a social action of the target person (e.g., "She told the secrets of a colleague to the others." *vs.* "She did not tell the secrets of a colleague to the others."). There were no differences between the positive and the negative sentences concerning the syntactic complexity as all sentences had a simple structure without any subordinate clauses and the same mean number of words in a sentence (mean number of words for both valence categories = 8.0; $T(22) < 1$, $p = 1.0$). Furthermore, semantic complexity was also comparable across the conditions as both valence categories did not differ in the mean word frequency per sentence according to the German vocabulary project of the University of Leipzig (http://wortschatz.uni-leipzig.de/; M for V+ = 651628.97, SD = 307675.20; M for V− = 713860.11, SD = 265210.25; $T(22) < 1$, $p = .60$).

Nonverbal stimuli consisted of 12 positive (N+) and 12 negative (N−) animated video files presenting a virtual character sitting in a chair and displaying different kinds of social signals. To optimize the control of the displayed nonverbal behavior and to minimize the impact of the physical appearance, we used anthropomorphic virtual characters as social stimuli (see Fig. 1). This approach was proved to be an internally as well as externally valid method to test the impact of nonverbal cues on person perception in behavioral (Bente, Feist, & Elder, 1996; Bente, Kraemer, Petersen, & de Ruiter, 2001; Bente, Petersen, Kraemer, & de Ruiter, 2001; Bente, Senokozlieva, Pennig, Al-Issa, & Fischer, 2008) and functional neuroimaging studies (Kuzmanovic et al., 2009; Moser et al., 2007; Schilbach et al., 2009; Schilbach et al., 2006). The design and animation of nonverbal behavior of the virtual character and the creation of the videos were realized by using the software package 'Poser 6' (Curious Labs, Inc. and e frontier, Inc.). In the initial, default sitting position, the virtual character exhibited a straight body

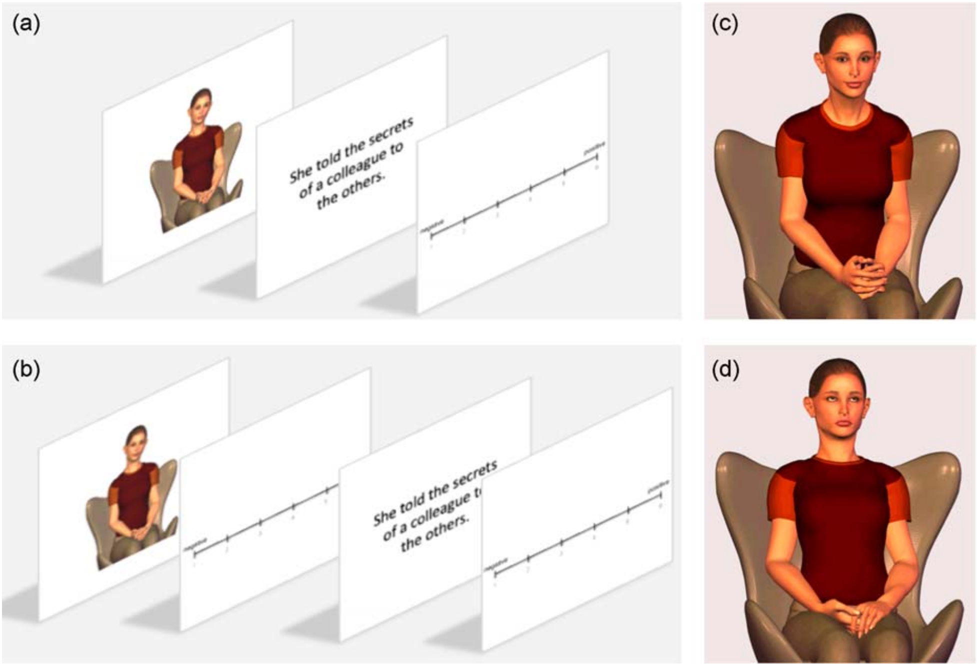

Fig. 1. Experimental procedure and examples of nonverbal stimuli. (a) An experimental trial from the complex impression formation task basing on a combination of verbal and nonverbal information. (b) An experimental trial from the basic impression formation task basing on single peaces of information providing a subjective evaluation of all stimuli. (c) An example of a positive nonverbal stimulus showing the target person displaying a direct gaze, smile and forward-lean. (d) An example of a negative nonverbal stimulus showing the target person rolling her eyes upwards, making an angry face and leaning backwards.

and head position with a neutral facial expression and a trunk rotated 10° to the right in order to increase the salience of observer-directed signals like direct gaze. This default position was systematically combined with four effective social signals, namely: (i) gaze direction (gaze directed to the observer *vs.* gaze directed upwards); (ii) facial expression (smile *vs.* angry face); (iii) body movement (forward-lean *vs.* backward-lean); and (iv) head movement (lateral flexion towards *vs.* away from the observer) (see Fig. 1c and d). These basic signals were then implemented as short movies under systematic variation of one (e.g., only the smile was displayed by the virtual character, i.e., single combination), two (e.g., the smile and the gaze directed to the observer were displayed by the virtual character, i.e., double combination), or three signals (e.g., smile, direct gaze, forward-lean, i.e., triple combination) resulting in 14 positive and 14 negative movies. Of these 28 movies and 28 sentences, the 12 most effective negative and 12 most effective positive sentences and movies (including 4 single, 4 double and 4 triple combination movies of positive and negative valence) were selected based on the results of a behavioral pilot study prior to the begin of the study. Consequently, the two positive and the two negative verbal and nonverbal stimuli, that evoked the weakest positive or negative impression formation, were excluded.

2.3. Procedure

The experiment consisted of two parts: (i) during the first part *complex* impression formation was to be performed based on a combination of verbal and nonverbal information and (ii) during the second part *basic* impression formation based on a single piece of information, either verbal or nonverbal, was required, providing a subjective evaluation of all stimuli for each participant (see Fig. 1a and b). Before each part, subjects were familiarized with the task by means of a standardized, computerized instruction that included practice trials with stimuli not used in the experimental tasks.

In the complex task, participants were instructed to judge female job applicants as positive or negative on a 6-point rating scale (1 = very negative; 2 = negative; 3 = rather negative; 4 = rather positive; 5 = positive; 6 = very positive) after a verbal and a nonverbal piece of information about this applicant had been shown. Verbal information was introduced as a statement by a friend of the target person in reference to her prior work place. Nonverbal information was said to be a representative scene of the face-to-face job interview overlayed onto a virtual character. In the basic task, the subjects were instructed to judge female job applicants on the same 6-point scale again, but this time based on either verbal or nonverbal information alone.

All stimuli were presented for 3 s with a 3 s break in between and a rating scale lasting for 2 s. Subsequent trials were separated by a 6 s break in the complex task and by a 3 s break in the basic task. Resulting trial length for the complex task, therefore, was 20 s and for the basic task 11 s. The complex task comprised 48 trials (12 V−N−, 12 V−N+, 12 V+N−, 12 V+N+) in a pseudorandomized order and lasted 16 min in total. Consequently, verbal and nonverbal information was either presented congruently (V−N− or V+N+) or incongruently (V−N+ or V+N−). Each stimulus was presented twice: once in the congruent and once in the incongruent condition. The sequence order of information (V/N *vs.* N/V) was fully counterbalanced across conditions. Verbal and nonverbal stimuli were presented in a fixed pattern, i.e., sentence–movie pairs were consistent across all subjects. The basic task also comprised 48 pseudorandomly ordered trials (12 V−, 12 V+, 12 N−, 12 N+) and lasted 8.8 min in total. Stimulus presentation and response recording were performed by using the software package Presentation 11.3 (Neurobehavioral Systems, Inc., www.neurobs.com/).

2.4. Analyses

The data were analyzed using the statistical software SPSS (SPSS Statistics 17.0). In all analyses a mixed design analysis of variance (ANOVA) with one between-subject independent variable *group* (HFA *vs.* control) and varying within-subject independent variables as described in the following was used.

For the complex task the analysis was separated into two ANOVAs distinguishing between congruent and incongruent combinations of verbal and nonverbal information. Congruent trials required no integration of conflicting information as necessary in incongruent trials allowing for the estimation of the relative impacts of verbal and nonverbal sources of information on impression formation. In both analyses, the within-subject factor was the *valence* of the combined information (congruent: positive (V+N+) *vs.* negative (V−N−); incongruent: positive verbal and negative nonverbal (V+N−) *vs.* negative verbal and positive nonverbal (V−N+). The dependent variables were the mean ratings for the relevant conditions (V+N+, V−N− and V−N+, V+N−) for each subject.

The same information can have varying meanings for different subjects. In order to investigate the relative influence of the different information domains based on the subjective evaluation of applied verbal and nonverbal stimuli, the ratings given in incongruent trials (V−N+ and V+N−) were related to the ratings of the respective single stimuli as acquired in the basic task where all stimuli were judged separately. The relative impact of the two domains on the complex impression formation was estimated by the absolute amount of the difference between the complex judgment (e.g., based on V−N+) and basic judgments based on the corresponding single stimuli (e.g., V− and N+). For instance, when the complex rating for a stimulus combination V−N+ was 2 and the basic ratings for the corresponding V− stimulus was 1 and for the corresponding N+ stimulus 5, the verbal stimulus exhibits a smaller distance to the complex rating ($|1-2| = 1$), and was therefore assumed to have a stronger impact in the decision-making process than the nonverbal stimulus whose basic rating exhibits a greater distance to the complex rating ($|5-2| = 3$). The raw data of these difference values from each participant were then averaged within the four possible conditions (mean relative impact of V−, V+, N− and N+). In order to obtain a more intuitive scaling of the dependent variable where higher scores correspond to greater relative impact, the mean relative impact scores were reversed by subtracting each score from the highest score obtained in the entire measured sample of HFA and control participants ($X_{\text{highest}} - X_i$). The ANOVA included the within-subject factors *domain* of the information (V *vs.* N) and *valence* of the information (+ *vs.* −) resulting in a two by two matrix.

Finally, in order to calculate the evaluation of single stimuli, impression ratings from the basic task were analyzed by defining the within-subject factors *domain* of the information (V *vs.* N) and *valence* of the information (+ *vs.* −) resulting in a two by two matrix (V−, V+, N− and N+). As in the complex task, the dependent variable was the mean rating for each of the four conditions for each individual participant.

In all analyses, the assumption of the normal distribution of the data was fulfilled for both groups and for all levels of the respective repeated-measures variables as indicated by the Kolmogorov–Smirnov-Test. Furthermore, the assumption of the homogeneity of variance for all levels of the repeated-measures variables was fulfilled as shown by the Levene's test. All effects are reported as significant at $p < .05$ (all *t*-tests were computed as two-tailed tests). Significant interactions were further analyzed using paired or independent sample *t*-tests.

3. Results

3.1. Basic impression formation

As shown in Table 2a and as plotted in Fig. 2a, there was no significant main effect of the factor group within the basic impression formation task indicating that there were no general differences with respect to the capacity to evaluate isolated verbal and nonverbal stimuli between the HFA and the control participants. Furthermore, there was no significant main effect of the factor domain showing that in general verbal and nonverbal information did not elicit

Table 2
Inferential statistics for the effects of interest.

Effects of interest and pair-wise comparisons	*F*/*t*	*p*	*r*	Mean difference	95% CI of mean difference	
					Lower bound	Upper bound
(a) **Basic impression formation**						
Group	.36	.552	.11	−.047	−.21	.11
Domain	.96	.335	.18	.08	−.08	.25
Valence	534.33	.000*	.97	−2.52	−2.74	−2.30
Valence × Domain	29.20	.000*	.71			
−: V vs. N	*−3.47*	*.002**	*.54*	*−.55*	*−.87*	*−.23*
+: V vs. N	*5.53*	*.000**	*.72*	*.71*	*.45*	*.98*
V: − vs. +	*−18.20*	*.000**	*.96*	*−3.15*	*−3.51*	*−2.80*
N: − vs. +	*−12.79*	*.000**	*.92*	*−1.89*	*−2.19*	*−1.59*
(b) **Complex impression formation**						
Congruent information						
Group	.06	.802	.05	.02	−.15	.19
Valence	617.40	.000*	.98	−3.14	−3.40	−2.88
Valence × group	.65	.428	.15			
Incongruent information						
Group	.00	.983	.00	.00	−.22	.22
Valence	40.01	.000*	.77	−1.52	−2.02	−1.03
Valence × group	6.54	.016*	.43			
V−N+: HFA vs. control	*−2.97*	*.006**	*.50*	*−.61*	*−1.04*	*−.19*
V+N−: HFA vs. control	*2.00*	*.056*	*.35*	*.62*	*−.02*	*1.25*
HFA: V−N+ vs. V+N−	*−6.25*	*.000**	*.86*	*−2.14*	*−2.87*	*−1.40*
Control: V−N+ vs. V+N−	*−2.68*	*.018**	*.58*	*−.91*	*−1.63*	*−.18*
(c) **Relative impact**						
Group	.15	.701	.07	.034	−.15	.21
Domain	23.33	.000*	.67	.75	.43	1.06
Valence	14.29	.001*	.58	.33	.15	.51
Domain × group	5.05	.033*	.39			
V: HFA vs. control	*2.47*	*.020**	*.42*	*.38*	*.07*	*.70*
N: HFA vs. control	*−1.58*	*.126*	*.29*	*−.31*	*−.71*	*.09*
HFA: V vs. N	*5.02*	*.000**	*.80*	*1.11*	*.63*	*1.58*
Control: V vs. N	*1.92*	*.076*	*.46*	*.41*	*−.05*	*.88*

HFA = high-functioning autism, *M* = mean, SD = standard deviation, CI = confidence interval, V = verbal information, N = nonverbal information, − = negative valence, + = positive valence. For the analyses (a) and (c) only the significant interactions are listed. In order to specify significant interaction effects, pair-wise comparisons by paired or independent sample *t*-tests were computed (italic font).

* Significant effects at a probability threshold $p < 0.05$.

differential impression ratings. There was a significant main effect of the factor valence demonstrating the general validity of the applied stimuli as positive stimuli were in fact rated as positive and negative stimuli as negative. However, there was also a significant interaction effect between the factors domain and valence revealing that verbal and nonverbal information was rated differentially when considering its valence. Pair-wise comparisons of negative information yielded stronger negative ratings of verbal as compared to nonverbal information (see Table 2a, −: V *vs.* N). Similarly, positive verbal information was perceived as more positive than positive nonverbal information (see Table 2a, +: V *vs.* N). Thus, although the difference between positive and negative stimuli within both the verbal and the nonverbal domain was highly significant and demonstrated a large effect size (see Table 2a, V:/N: − *vs.* +), this difference was greater within the verbal domain than within the nonverbal domain as evident from the mean difference and confidence intervals. Taken together, the statistical interaction between the factors domain and valence indicates that verbal and nonverbal stimuli are not strictly comparable concerning their potential to induce positive and negative impressions. At the same time, the validity of both verbal and nonverbal stimuli is still maintained as positive information always ranges within the positive levels of the rating scale (4–6) and negative information within the negative levels (1–3) even for the nonverbal information (see Fig. 2a). Still, it is possible and plausible that the difference in the potential to induce positive and negative impressions between the verbal and nonverbal information could interfere with the relative impact of these two modalities within combined incongruent information trials, which needs to be considered in the discussion of these effects. However, as there were no significant interaction effects between the factors group and valence ($F(1, 28) < 1$, $p = .42$), nor group and domain ($F(1, 28) < 1$, $p = .91$), nor group, valence and domain ($F(1, 28) = 2.00$, $p = .17$), no constraints need to be made for the discussion of the group related differences in the integrative rating of combined information.

3.2. Complex impression formation

As shown in Table 2b and plotted in Fig. 2b, for *both* congruent and incongruent combinations of verbal and nonverbal information there was no significant main effect of the factor group indicating that ratings of HFA and control participants were in general the same, i.e., when disregarding the effects of the valence of stimuli.

For *congruent* trials there was, similar to basic impression formation, a significant main effect of the factor valence of the combined information showing that positive information combinations were rated more positively than negative information combination. There was no significant interaction effect between the factors group and valence indicating that both groups made a similar distinction between positive and negative congruent information.

For *incongruent* trials there was also a significant main effect of the factor valence of the combined information showing that V−N+ trials were rated more negative than V+N− trials indicating a more robust influence of the verbal domain on the complex impression formation within incongruent trials. Furthermore, there was a significant interaction effect between the factors group and valence. Pair-wise comparisons revealed that HFA participants rated the V−N+ trials significantly more negative and the V+N− trials as more positive on a trend level, both in comparison to control subjects (see Table 2b, incongruent information, V−N+:/V+N−: HFA *vs.* control). This indicates that although both groups relied more on the verbal information, this effect is pronounced stronger in the HFA group because the mean ratings are influenced stronger by the valence of the verbal information. Consistent with this finding, the difference in the HFA group between V−N+ and V+N− is significantly greater than in the control group as demonstrated by the differences in effect sizes as well as by the mean differences and the confidence intervals (see Table 2, incongruent information, HFA:/control: V−N+ *vs.* V+N−). For the HFA group the latter include only mean strong differences while in the control group small mean differences are comprised as well.

3.3. Relative impact

In a supplementary analysis we calculated the relative impacts of positive and negative verbal and nonverbal information within complex incongruent trials in reference to the basic evaluation of the corresponding single stimuli for each participant (see Section 2.4). Again, as shown in Table 2c and plotted in Fig. 2c there was no main effect of the factor group confirming that in general the stimuli had a comparable influence on impression formation in HFA and control participants, i.e., when disregarding the effects of domain and valence. There was a significant main effect of the factor valence demonstrating a greater impact of negative as compared to positive information, irrespective of group or domain. As there was no significant interaction effect between the factors group and valence ($F(1,28) < 1$, $p = .60$) both groups appeared to show the same tendency in that they take negative information more into consideration than positive information. Also, there was a significant main effect of the factor domain, which indicates that verbal information had a greater impact on the impression formation than nonverbal information. Importantly, this effect differed between the groups, as there was a significant interaction between the factors group and domain. Pair-wise comparisons revealed that HFA participants relied more on the verbal information than control participants (see Table 2c, V: HFA *vs.* Control). Crucially, the difference between the relative impact of verbal and nonverbal information was significant and large in the HFA (see Table 2c, HFA: V *vs.* N), but not in the control group (see Table 2c, control: V *vs.* N). Finally, there was no significant interaction effect between the factors valence and domain ($F(1,28) < 1$, $p = .58$) nor group, domain and valence ($F(1,28) < 1$, $p = .77$).

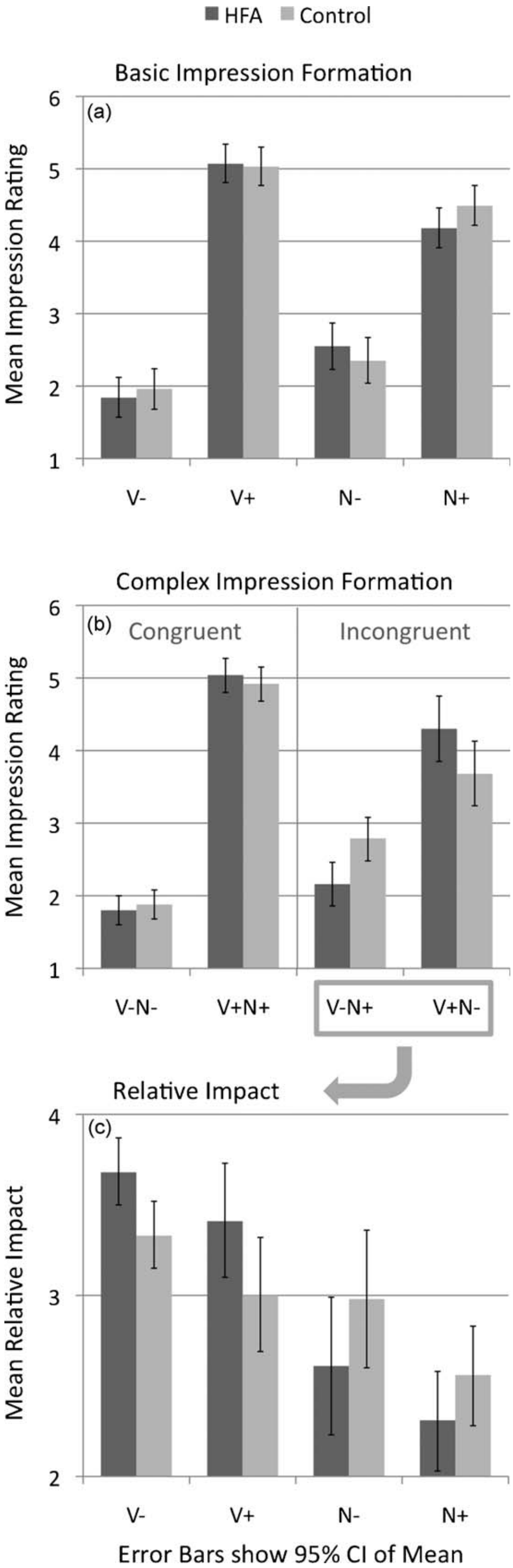

Fig. 2. Bar graphs showing results of the impression formation tasks for the HFA and control group. (a) Mean ratings for the basic impression formation based on a single peace of information; (b) mean ratings for the complex impression formation based on a combination of verbal and nonverbal information

4. Discussion

The present study sought to investigate the differential impact of verbal and nonverbal information on impression formation in HFA. When presenting the socially relevant information independently or in congruent combinations, no significant differences between the HFA and the matched control group were observed. Furthermore, when presenting contradicting verbal and nonverbal information, both groups exhibited a tendency to more strongly rely on verbal information. Importantly, however, impression formation of the HFA participants was more strongly influenced by verbal information than that of the control group. In addition, by proceeding from the subjective evaluations of the underlying stimuli to assess the relative influence of the information domains, we were able to demonstrate a relative dominance of the verbal over the nonverbal domain only within the HFA but not within the control group. While both verbal and nonverbal stimuli had a considerable influence on control participants indicating an integration of the relevant social information, the HFA participants showed a bias towards relying on the verbal domain thereby neglecting the nonverbal cues.

The first finding that there were no group differences in evaluating isolated verbal or nonverbal information contradicts our a priori hypothesis. It demonstrates that HFA individuals are well able to detect and interpret socially relevant cues from both domains to form an impression, when explicitly instructed to do so and when engaged in a simplified and structured task. However, the degree to which nonverbal information contributes to complex subjective social decisions is significantly lower in HFA than in control participants. This finding points towards differences in the impact of the two information domains detectable only when contextualizing nonverbal cues within other relevant and competing sources of information. Based on the finding that individuals with HFA are able to infer personality traits from textual action descriptions (Ramachandran, Mitchell, & Ropar, 2009), we suppose that such deductive social constructs might guide individuals with HFA when evaluating the target person based on verbal stimuli. In contrast, dynamic nonverbal behavior might be less clearly related to certain social constructs and might influence the global impression formation by means of an immediate 'value' of the observed social cues (Bente & Kraemer, 2003, 2008; Kraemer, 2008). We suggest that during the complex impression formation, nonverbal information needs not only to be identified, but must also lead to the formation of an affectively meaningful impression that is able to bias the representations of additional verbal information. As previous results from our group could demonstrate that nonverbal information has less influence on feelings in HFA (Schwartz, Bente, Gawronski, Schilbach, & Vogeley, 2010), we suggest an impoverished affective response to nonverbal stimuli in people with HFA. Thus, for HFA individuals, nonverbal information does not seem to leave a profound impression and, therefore, can hardly become effective in the context of explicit verbal information. Consequently, there seems to be a dissociation between *knowing* what a cue means on the one hand, and, on the other hand, *acting* upon it based on motivational predispositions to respond to salient social stimuli (Klin, Jones, Schultz, & Volkmar, 2003).

An alternative explanation for the less effective performance of the HFA group in the complex task could be provided by its increased difficulty relative to the basic task. When defining the difficulty by the quantity of information, then this explanation can be disproved because HFA participants did not differ from the controls in the complex congruent task, which also required the consideration of two pieces of information. However, the difficulty can also be defined by the quality of information, i.e., by the fact that the information was contradictory in the complex incongruent task. Even so, if the increased difficulty would have been the only reason for the differences in the performance of the task, then the reduced ability to integrate multiple contradictory information should have affected both domains equally, but not specifically the nonverbal domain. In conclusion, we argue that the increased difficulty of the complex incongruent task alone cannot sufficiently explain the reduced influence of the nonverbal information.

On a more speculative note, the good performance in the basic task along with the stronger reliance on the verbal information in the complex incongruent task might indicate an essential difference in the underlying cognitive processes between the HFA and the control group. It could be possible that HFA participants apply a more analytic processing style when dealing with social information. Thus, they could more easily deal with the verbal information and would be able to apply rule-based processing for the simple decoding of the nonverbal information only in the absence of competing verbal information. Providing only a weak basis for stringent logical reasoning, social decisions and impressions that incorporate multimodal and also incomplete, ambiguous or even contradictory information could profit from more intuitive, spontaneous processing (De Martino, Harrison, Knafo, Bird, & Dolan, 2008). Supporting this suggestion, individuals with HFA showed prolonged reaction times in face discrimination tasks along with preserved accuracy (Behrmann et al., 2006) suggesting the employment of cognitive processes that require a higher effort. Furthermore, functional neuroimaging studies have revealed atypical strategies for face perception in HFA adults indicated by the recruitment of neural regions associated with object but not with face recognition – despite of high accuracy on the behavioral level (Critchley et al., 2000; Schultz et al., 2000). Consequently, although being perfectly able to process nonverbal signals under simplified laboratory conditions, HFA individuals are likely to be less effective in their everyday social interactions or in more complex experimental settings failing to respond in a fast and spontaneous way (Frith, 2003; Klin et al., 2003; Senju, Southgate, White, & Frith, 2009).

separated for congruent and incongruent trials; and (c) mean relative impact of verbal and nonverbal information within complex trials with incongruent peaces of information. The scaling on the *y*-axis refers in (a) and (b) to the rating scale ranging from 1 (very negative impression) to 6 (very positive impression) and in (c) to the relative effects computed in reference to basic evaluation of the corresponding stimuli.

Finally, our results revealed interesting overall effects for both groups within the incongruent complex impression formation task. Firstly, both groups equally attached greater importance to information with a negative valence. This tendency is also known as the ‘negativity effect’, which has frequently been demonstrated in the impression formation research (Skowronski & Carlston, 1989). According to this notion, negative information is perceived as more ‘diagnostic’ for trait inferences because it contradicts the social norms and is thus perceived as more closely related to intrinsic motivation and personality characteristics of the target person (Jones & Davis, 1965). Secondly, when building an impression based on conflicting verbal and nonverbal information, both the HFA and the control group tended to rely more on the verbal information even though this bias was significantly stronger in the HFA group. Importantly, this dominance of verbal information needs to be considered in the context of the greater distinctiveness of negative and positive verbal stimuli in comparison to nonverbal stimuli as assessed in the basic impression formation task across both groups. We suggest that the higher potential to induce positive and negative impressions of verbal stimuli may underlie the greater general impact of verbal information within the incongruent complex impression formation. Accordingly, it is crucial to take into account the subjective evaluation of the corresponding single pieces of information when assessing the relative influence of the verbal and nonverbal domain. With this procedure it was, indeed, possible to account for the variance of the stimulus material underlying the complex impression formation with respect to the potential to evoke subjective positive or negative impressions and to reveal more robust differences between the groups concerning the relative impact of verbal and nonverbal stimuli.

5. Conclusions

Taken together, HFA individuals show a tendency to rely more strongly on the explicit, verbal domain when forced to integrate conflicting social stimuli. Although they are able to decode the meaning of isolated nonverbal information, HFA participants were significantly less influenced by the same nonverbal cues when making complex social decisions. The nature of cognitive processes that underlie the evaluation of socially relevant verbal and nonverbal information, however, remain an open question and could be addressed by making use of experimental set-ups enriched by psycho-physiological and functional neuroimaging methods in future research.

Acknowledgments

BK was supported by a grant from the German Ministry of Education and Research (Project ‘‘Other Minds’’, grant 01 GP 0802). LS was supported by the Koeln Fortune Program of the Medical Faculty, University of Cologne. We thank K. Volpert, U. Behrendt and S. Morell for neuropsychological testing.

References

Baron-Cohen, S. (2003). *The essential difference: The truth about the male and female brain*. New York, NY: Basic Books.

Baron-Cohen, S., Ring, H. A., Wheelwright, S., Bullmore, E. T., Brammer, M. J., Simmons, A., et al. (1999). Social intelligence in the normal and autistic brain: An fMRI study. *European Journal of Neuroscience, 11*, 1891–1898.

Beck, A. T., & Steer, R. A. (1987). *Beck depression inventory – manual*. San Antonio: The Psychological Corporation.

Behrmann, M., Avidan, G., Leonard, G. L., Kimchi, R., Luna, B., Humphreys, K., et al. (2006). Configural processing in autism and its relationship to face processing. *Neuropsychologia, 44*, 110–129.

Bente, G., Feist, A., & Elder, S. (1996). Person perception effects of computer-simulated male and female head movement. *Journal of Nonverbal Behavior, 20*, 213–228.

Bente, G., & Kraemer, N. C. (2003). Die integrierte Registrierung verbalen und nonverbalen Kommunikationsverhatens. In Herrmann, T., & Grabowski, J. (Eds.), *Sprachproduktion*. (pp.219–246).

Bente, G., & Kraemer, N. C. (2008). Effects of nonverbal communication. In Donsbach, W. (Ed.). *International encyclopedia of communication*. (pp.3334–3339).

Bente, G., Kraemer, N. C., & Eschenburg, F. (2008). Is here anybody out there? Analyzing the effects of embodiment and nonverbal behavior in avatar-mediated communication. In Konijn, E., Utz, S., Tanis, M., & Barnes, S. (Eds.), *Mediated interpersonal communication*. (pp.131–157).

Bente, G., Kraemer, N. C., Petersen, A., & de Ruiter, J. P. (2001). Computer animated movement and person perception: Methodological advances in nonverbal behavior research. *Journal of Nonverbal Behavior, 25*, 151–166.

Bente, G., Petersen, A., Kraemer, N. C., & de Ruiter, J. P. (2001). Transcript-based computer animation of movement: Evaluating a new tool for nonverbal behavior research. *Behavior Research Methods, Instruments, and Computers, 33*, 303–310.

Bente, G., Senokozlieva, M., Pennig, S., Al-Issa, A., & Fischer, O. (2008). Deciphering the secret code: A new methodology for the cross-cultural analysis of nonverbal behavior. *Behavior Research Methods, 40*, 269–277.

Burgoon, J. K. (1994). Nonverbal signals. In Knapp, M. L., & Miller, G. R. (Eds.), *Handbook of interpersonal communication*. (pp.229–285).

Choi, V. S., Gray, H. M., & Ambady, N. (2005). The glimpsed world: Inintended communication and unintended perception. In Hassin, R. R., Uleman, J. S., & Bargh, J. A. (Eds.), *The new unconcsious*. (pp.309–333).

Critchley, H. D., Daly, E. M., Bullmore, E. T., Williams, S. C., Van Amelsvoort, T., Robertson, D. M., et al. (2000). The functional neuroanatomy of social behaviour: Changes in cerebral blood flow when people with autistic disorder process facial expressions. *Brain, 123*, 2203–2212.

De Martino, B., Harrison, N. A., Knafo, S., Bird, G., & Dolan, R. J. (2008). Explaining enhanced logical consistency during decision making in autism. *Journal of Neuroscience, 28*, 10746–10750.

Domangue, B. B. (1978). Decoding effects of cognitive complexity, tolerance of ambiguity, and verbal–nonverbal inconsistency. *Journal of Personality, 46*, 519–535.

Droney, J. M., & Brooks, C. I. (1993). Attributions of self-esteem as a function of duration of eye contact. *Journal of Social Psychology, 133*, 715–722.

Evans, J. S. (2008). Dual-processing accounts of reasoning, judgment, and social cognition. *Annual Review of Psychology, 59*, 255–278.

Frey, S. (1999). *Die Macht des Bildes*. Bern, Germany: Huber.

Frith, U. (2003). *Autism: Explaining the enigma*. Oxford: Basil Blackwell.

Gilbert, D. T., & Krull, D. S. (1988). Seeing less and knowing more: The benefits of perceptual ignorance. *Journal of Personality and Social Psychology, 54*, 193–202.

Grammer, K., Honda, M., Juette, A., & Schmitt, A. (1999). Fuzziness of nonverbal courtship communication unblurred by motion energy detection. *Journal of Personality and Social Psychology, 77*, 487–508.

Jones, E. E., & Davis, K. E. (1965). From acts to dispositions: The attribution process in person perception. In Berkowitz, L. (Ed.). *Advances in experimental social psychology*. Vol. 2 (pp.219–266)New York: Academic Press.

Klin, A., Jones, W., Schultz, R., & Volkmar, F. (2003). The enactive mind, or from actions to cognition: Lessons from autism. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 358*, 345–360.

Kraemer, N. C. (2008). Nonverbal communication. In Blascovich, J. J., & Hartel, C. R. (Eds.), *Human behavior in military contexts*. (pp.150–188).

Kuzmanovic, B., Georgescu, A. L., Eickhoff, S. B., Shah, N. J., Bente, G., Fink, G. R., et al. (2009). Duration matters: Dissociating neural correlates of detection and evaluation of social gaze. *Neuroimage, 46*, 1154–1163.

Lehrl, S., Triebig, G., & Fischer, B. (1995). Multiple choice vocabulary test MWT as a valid and short test to estimate premorbid intelligence. *Acta Neurologica Scandinavica, 91*, 335–345.

Levine, S. P., & Feldman, R. S. (2002). Women and men's nonverbal behavior and self-monitoring in a job interview setting. *Applied H.R.M. Research, 7*, 1–14.

Moser, E., Derntl, B., Robinson, S., Fink, B., Gur, R. C., & Grammer, K. (2007). Amygdala activation at 3T in response to human and avatar facial expressions of emotions. *Journal of Neuroscience Methods, 161*, 126–133.

Ramachandran, R., Mitchell, P., & Ropar, D. (2009). Do individuals with autism spectrum disorders infer traits from behavior? *The Journal of Child Psychology and Psychiatry, 50*, 871–878.

Scherer, K. R., Scherer, U., Hall, J. A., & Rosenthal, R. (1977). Differential attribution of personality based on multi-channel presentation of verbal and nonverbal cues. *Psychological Research, 39*, 221–247.

Schilbach, L., Wilms, M., Eickhoff, S. B., Romanzetti, S., Tepest, R., Bente, G., et al. (2009). Minds made for sharing: Initiating joint attention recruits reward-related neurocircuitry. *Journal of Cognitive Neuroscience* .

Schilbach, L., Wohlschlaeger, A. M., Kraemer, N. C., Newen, A., Shah, N. J., Fink, G. R., et al. (2006). Being with virtual others: Neural correlates of social interaction. *Neuropsychologia, 44*, 718–730.

Schmidt, K. H., & Metzler, P. (1992). *Wortschatztest (WST)*. Weinheim: Beltz Test GmbH.

Schultz, R. T., Gauthier, I., Klin, A., Fulbright, R. K., Anderson, A. W., Volkmar, F., et al. (2000). Abnormal ventral temporal cortical activity during face discrimination among individuals with autism and Asperger syndrome. *Archives of General Psychiatry, 57*, 331–340.

Schwartz, C., Bente, G., Gawronski, A., Schilbach, L., & Vogeley, K. (2010). Responses to nonverbal behaviour of dynamic virtual characters in high-functioning autism. *Journal of Autism and Developmental Disorders, 40*, 100–111.

Senju, A., Southgate, V., White, S., & Frith, U. (2009). Mindblind eyes: An absence of spontaneous theory of mind in Asperger syndrome. *Science, 325*, 883–885.

Skowronski, J. J., & Carlston, D. E. (1989). Negativity and extremity biases in impression formation: A review of explanations. *Psychological Bulletin, 105*, 131–142.

Stewart, M. E., Barnard, L., Pearson, J., Hasan, R., & O'Brien, G. (2006). Presentation of depression in autism and Asperger syndrome: A review. *Autism, 10*, 103–116.

Suslow, T. (2009). Estimating verbal intelligence in unipolar depression: Comparison of word definition and word recognition. *Nordic Journal of Psychiatry, 63*, 120–123.

Wheelwright, S., Baron-Cohen, S., Goldenfeld, N., Delaney, J., Fine, D., Smith, R., et al. (2006). Predicting Autism Spectrum Quotient (AQ) from the Systemizing Quotient-Revised (SQ-R) and Empathy Quotient (EQ). *Brain Research, 1079*, 47–56.

NeuroImage 60 (2012) 179–188

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Imaging first impressions: Distinct neural processing of verbal and nonverbal social information

Bojana Kuzmanovic [a,b,*], Gary Bente [c], D. Yves von Cramon [d], Leonhard Schilbach [d,a], Marc Tittgemeyer [c], Kai Vogeley [a,e]

[a] *Department of Psychiatry and Psychotherapy, University Hospital Cologne, Germany*
[b] *Institute of Neurosciences and Medicine — Ethics in the Neurosciences (INM-8), Research Center Juelich, Germany*
[c] *Department of Psychology, University of Cologne, Germany*
[d] *Max-Planck Institute for Neurological Research, Cologne, Germany*
[e] *Institute of Neurosciences and Medicine — Cognitive Neurology (INM-3), Research Center Juelich, Germany*

ARTICLE INFO

Article history:
Received 8 July 2011
Revised 12 December 2011
Accepted 15 December 2011
Available online 27 December 2011

Keywords:
Amygdala
Posterior cingulate cortex
Verbal
Nonverbal
Impression formation
Person perception

ABSTRACT

First impressions profoundly influence our attitudes and behavior toward others. However, little is known about whether and to what degree the cognitive processes that underlie impression formation depend on the domain of the available information about the target person. To investigate the neural bases of the influence of verbal as compared to nonverbal information on interpersonal judgments, we identified brain regions where the BOLD signal parametrically increased with increasing strength of evaluation based on either short text vignettes or mimic and gestural behavior. While for verbal stimuli the increasing strength of subjective evaluation was correlated with increased neural activation of precuneus and posterior cingulate cortex (PC/PCC), a similar effect was observed for nonverbal stimuli in the amygdala. These findings support the assumption that qualitatively different cognitive operations underlie person evaluation depending upon the stimulus domain: while the processing of nonverbal person information may be more strongly associated with affective processing as indexed by recruitment of the amygdala, verbal person information engaged the PC/PCC that has been related to social inferential processing.

Introduction

In our everyday life we are ready to make fast and spontaneous judgments about other persons (Uleman et al., 2008), which are determined by our very subjective evaluation of the available information about the target person (Schiller et al., 2009). Furthermore, first impressions are mostly not restricted to inferences about enduring dispositions, e.g., that someone is intelligent because he passed a math test, but also encompass an evaluative component due to the assignment of a rather positive or negative value to someone's individual characteristics. Importantly, the outcome of such an evaluation crucially determines our expectations and behavior toward social others (Delgado et al., 2005; Uleman et al., 2008).

However, little is known about whether the cognitive processes mediating the evaluation of another person differ depending upon the domain of available information. While the traditional person judgment research has relied on verbal stimuli such as action description or trait adjectives, short excerpts of nonverbal behavior have been demonstrated to be equally effective in evoking differentiated assessments (Ambady et al., 2000; Kuzmanovic et al., 2011). But although ratings of other persons may lead to similar outputs across different domains of information, this does not allow for inferences regarding the degree of similarity of underlying cognitive processes. However, comparing the neural correlates of impression formation that relies on verbal and nonverbal person information, respectively, could be used as an index for such conclusions. Thus, the present study explores putative differences in the neural signature of the evaluative component of impression formation dependent upon whether the underlying relevant social information was presented verbally or nonverbally. Given the far-reaching consequences of impression formation within social interactions, elucidating possible domain-specific differences in the related neural processing would extend the understanding of interpersonal behavior and might have significant implications for social decisions.

Theoretical considerations suggest divergent processing streams across domains by stating that language is digitally defined by an explicit semantic code with a complex logical syntax, while the interpretation of analog nonverbal signals appears to be more uncertain as multiple cues may occur simultaneously and extend over time, and are known to have greater impact on the affective, relational level of communication (Kraemer, 2008; Watzlawick et al., 1967). Supporting these assumptions, a recent neuroimaging study indeed

---

* Corresponding author at: Department of Psychiatry and Psychotherapy, University Hospital Cologne, Germany. Fax: +49 221 478 87702.
E-mail address: bojana.kuzmanovic@uk-koeln.de (B. Kuzmanovic).

1053-8119/$ – see front matter © 2012 Elsevier Inc. All rights reserved.
doi:10.1016/j.neuroimage.2011.12.046

has demonstrated domain-specific neural systems involved when drawing inferences about social targets' affective states: while verbal information processing was associated with the mental state attribution system including the dorsomedial prefrontal cortex (dmPFC), precuneus (PC), temporopolar and temporoparietal regions, the nonverbal information processing related to the right inferior frontoparietal network corresponding to the putative human mirror neuron system, bilateral amygdala, right superior temporal sulcus (STS) and fusiform gyrus (FFG) (Zaki et al., 2010). Direct comparisons between verbal and nonverbal stimuli though cannot identify specific differences in social cognition because of additionally present basic differences in sensory and cognitive processing across domains.

In the specific context of interpersonal judgments, little is known about the neural processing of dynamic nonverbal behavior. However, studies using still neutral faces have provided consistent evidence for the amygdala being crucially involved in their evaluation with respect to judgments of trustworthiness and valence (Todorov, 2008; Todorov and Engell, 2008; Winston et al., 2002). Although being generally associated with salience detection, and with assigning an emotional value to external cues, the response of the amygdala appears to be particularly sensitive for faces that convey significant social cues (Hariri et al., 2002; Sergerie et al., 2008). In contrast, the processing of verbal person information in the context of interpersonal judgments has been consistently associated with the dmPFC (Harris et al., 2005; Mitchell et al., 2002, 2005; Ochsner et al., 2005; Sugiura et al., 2004; Zysset et al., 2002). While this is in concordance with its central role in mental state attribution and person perception (Amodio and Frith, 2006), it has recently been demonstrated that the dmPFC is not specifically involved in evaluative processes of impression formation (Schiller et al., 2009). Instead, evaluation of others has been shown to differentially engage the amygdala and the posterior cingulate cortex (PCC), which were activated stronger by stimuli that guided subsequent judgments (Schiller et al., 2009). Additionally, these regions also exhibited increases in the BOLD signal with increasing strength of the evaluative judgment (Schiller et al., 2009). The study by Schiller and colleagues, however, failed to investigate putative stimulus domain-specific differences as they used simultaneously both verbal and nonverbal stimuli. Our study was conducted to directly address this aspect: Specifically, we were interested in exploring differences in neural processing of verbal and nonverbal social information, which evokes increasing strengths of evaluative person judgment.

Using functional magnetic resonance imaging (fMRI), we employed an experimental paradigm containing verbal (V) and nonverbal (NV) stimuli of different valences (positive, negative, and neutral). Participants were instructed to rate target persons along a global positive–negative scale based on either a) a short video clip showing an animated virtual character displaying dynamic expressive nonverbal behavior; or b) short verbal action description. Additionally, the arousal of all stimuli was assessed after scanning in order to control for this dimension of person perception. We aimed to identify brain regions whose activity correlated with the ‘strength’ of subsequent evaluations of social others based either on verbal or nonverbal information (operationalized as a difference from 0 on the rating scale, i.e., including both positive and negative judgments). Notably, we based this analysis on individual responses in order to take into account that the same piece of information can have different meanings or values for different persons. We expected that brain regions, which are involved in the evaluation of others, would increase their activation with increasingly pronounced impressions. By focusing on the parametric modulation of the neural activity by the ‘strength of evaluation’ (SoE), this paradigm allows to compare different domains, in spite of basic sensory and cognitive stimulus-specific processing differences. The SoE-effect was computed separately for each domain, so that across all events the basic stimulus characteristics were identical and differences related only to the degree to which they, in fact, influenced the subsequent evaluation of the target person.

Methods

Subjects

18 right-handed participants with no reported history of neurological or psychiatric illness were included in the study (9 males, mean age = 24.7, age range 21–29 years). All participants gave informed consent and were naïve with respect to the experimental task and the purpose of the study. The study was approved by the local ethics committee of the University Hospital Cologne.

Stimuli

Positive and negative verbal and nonverbal stimuli were created as reported in detail in Kuzmanovic et al. (2011). Verbal stimuli (V) consisted of sentences describing a social action suitable to induce an impression of a female target person (e.g., “She told the secrets of a colleague to the others.” vs. “She did not tell the secrets of a colleague to the others.”; see Fig. 1B). Nonverbal stimuli (NV) consisted of dynamic video clips of 3 s duration with an animated female virtual character displaying impression-evoking nonverbal signals. While using the same virtual character for all nonverbal stimuli, the following expressive features were systematically varied: Gaze direction (direct vs. averted gaze), facial expression (smile vs. angry face), body movements (forward vs. backward lean), and head movements (lateral vs. backward flexion) (see Fig. 1A). The purpose of the strict control of the target person's physical appearance was to ensure that both verbal and nonverbal stimuli conveyed individuated social information related to idiosyncratic behavior, which is not reducible to more superficial cues like face morphology or hair color. In addition, neutral verbal (non-social action descriptions: e.g., “She opened the drawer of her desktop.”) and nonverbal stimuli (non-expressive facial and body movements) were created in order to enable the comparison between impression-valent and impression-neutral stimuli. In each domain (V, NV), the three valence categories, i.e., negative (−), neutral (0) and positive (+), were matched for complexity. Verbal stimuli did not differ with regard to syntactic complexity as all sentences had a simple structure without any subordinate clauses and the same mean number of words (ANOVA of mean number of words per sentence for −, 0, +, $F(2,33) = .04$, $p = .96$). Furthermore, semantic complexity was also comparable across the valence conditions as there were no differences in the word frequency according to the German vocabulary project of the University of Leipzig (http://wortschatz.uni-leipzig.de/; ANOVA of mean word frequency per sentence for −, 0, +, $F(2,33) = .27$, $p = .76$). Finally, neutral, positive and negative nonverbal stimuli had the same quantity of movement as measured by the mean of frame-to-frame pixel change per stimulus (ANOVA, $F(2,33) = .40$, $p = .67$).

The stimuli were pretested in an independent sample ($n = 14$) with regard to ratings of valence (−3 = very negative to 3 = very positive) and arousal (−3 = not arousing to 3 = very arousing) resulting in mean ratings shown in Table 1. Paired *t*-tests revealed that positive verbal and nonverbal and negative verbal and nonverbal stimuli did not significantly differ regarding valence or arousal ratings ($p > .05$ for all comparisons). However, although neutral verbal and nonverbal stimuli were comparable concerning the valence ratings ($p > .05$), they differed with regard to arousal ratings ($t(13) = -2.85$, $p = .01$) with neutral verbal stimuli being rated as less arousing than neutral nonverbal stimuli.

Procedure

Stimulus presentation and response recording were performed by the software package Presentation (version 13.1; Neurobehavioral Systems, Inc). Stimuli were projected onto a screen (Optostim, 32-inch, resolution 1280×800) at the end of the magnet bore that

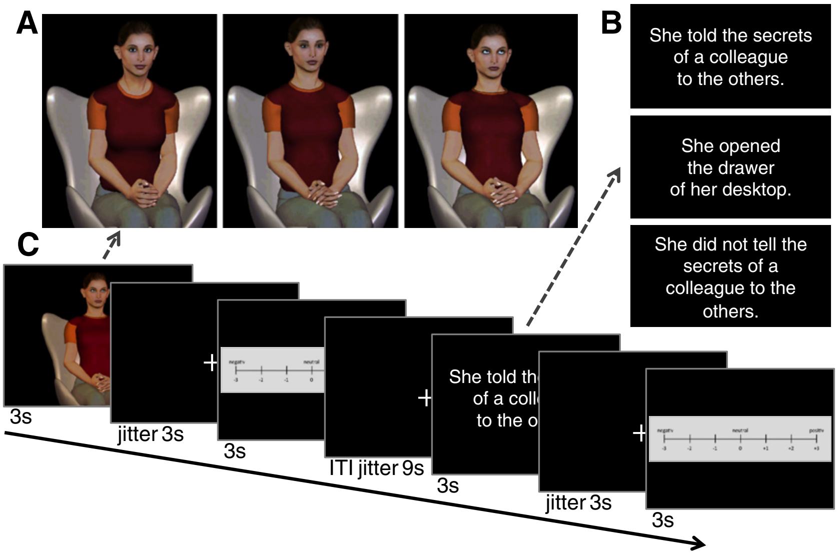

Fig. 1. Examples of verbal and nonverbal stimuli and the experimental procedure of the evaluative impression formation task. A) Example frames from positive, neutral and negative nonverbal video stimuli. B) Example sentences of positive, neutral and negative verbal stimuli. Originally, the sentences were on German, but are translated into English for illustration purposes. C) An example of two subsequent experimental trials: verbal and nonverbal stimuli with differing valences were presented in a randomized order and rated by participants on a 7-point global evaluation rating scale.

participants viewed via a mirror mounted to the head coil. Responses were assessed using a MR-compatible response device (Current Design).

Participants were instructed to judge female job applicants as positive or negative on a 7-point rating scale (−3 = very negative; −2 = negative; −1 = rather negative; 0 = neutral; 1 = rather positive; 2 = positive; 3 = very positive) based on either verbal or nonverbal information. A 7-point scale was used in order to enable participants to give neutral ratings as well. Verbal information was said to provide descriptions of the applicant's behavior toward colleagues at the prior workplace. Nonverbal information was said to be a “thin slice” of the applicant's behavior toward colleagues at the prior workplace. Participants were further instructed to treat the social referent across trials as different target persons. In other words, they were instructed to form a new impression on every trial independently of previously observed person information. It was explained that the nonverbal cues were overlayed on the same virtual character in order to control for effects of physical appearance on impression formation. An experimental trial consisted of a 3000 ms stimulus presentation (either V or NV) followed by a rating scale lasting for 3000 ms. Participants received a visual feedback about their button presses and could correct given responses if necessary until the end of the rating scale slide. Furthermore, each trial entailed two randomly jittered intervals with a fixation cross: one between each stimulus presentation and the following rating scale in order to enable a separate analysis of the person evaluation and the response (average duration 3000 ms, jittering between 1875 ms and 4125 ms) and the other between single trials to increase condition-specific BOLD signal discriminability (Serences, 2004) (average duration 9000 ms, jittering between 7875 ms and 10,125 ms). Taken together, an average trial lasted for 15,000 ms (see Fig. 1C). In total, the task consisted of 72 trials (36 stimuli for each of the two domains) that were presented in a randomized order within two sessions of 9 min duration each. In one session button presses were performed with the right and in the other session with the left hand, this sequence being randomized across participants. After scanning, participants underwent an additional task, in which they rated all stimuli on a 7-point rating scale measuring arousal.

Table 1
Descriptive statistics of the stimuli: Means and standard deviations of valence and arousal ratings from the pretest.

		−	0	+
Valence	V	−1.88 (.34)	.08 (.16)	2.03 (.27)
	NV	−2.08 (.63)	−.09 (.54)	1.76 (.32)
Arousal	V	1.45 (.98)	−1.66 (1.01)	.04 (1.23)
	NV	.96 (.86)	−.61 (.92)	.32 (.60)

fMRI acquisition

Functional and structural MRI images were acquired on a Siemens Magnetom Trio 3T whole-body scanner with a Tx/Rx birdcage coil. For the fMRI scans we used a T2*-weighted gradient echo planar imaging (EPI) sequence with the following imaging parameters: TR = 2200 ms, TE = 30 ms, FoV = 210, 33 oblique (maximal 30°) axial slices, and slice thickness = 3.0 mm. Two sessions of 301 images were acquired, preceded by 3 additional images allowing for T1 magnetic saturation effects that were discarded prior to further image processing. For the structural images we used high-resolution T1-weighted modified driven equilibrium Fourier transform sequence with the following parameters: TR = 1930 ms, TE = 5.8 ms, FoV = 256, 128 sagittal slices, and slice thickness = 1.25 mm.

fMRI preprocessing and analysis

Images were preprocessed and analyzed using MATLAB 7.1 (The MathWorks Inc) and SPM8 (The Wellcome Trust Center for Neuroimaging) as follows. After the EPI images were corrected for head movements using realignment and unwarping, the mean EPI image of each participant was computed and coregistered to the corresponding T1 image. The T1 image was then used to obtain normalization parameters for each participant to the Montreal Neurological Institute (MNI) reference space using the unified segmentation function in SPM8. The ensuing deformation was subsequently applied to the individual EPI volumes, the T1 image and the segmented T1 images with a writing resolution of 8 mm^3. The normalized EPI images were spatially smoothed using an 8 mm FWHM Gaussian kernel to meet the statistical requirements of further analysis and to compensate for macroanatomical variations across participants.

The data were analyzed using a General Linear Model as implemented in SPM8. The following specifications apply to all conducted analyses. Conditions were modeled using a boxcar reference vector convolved with the canonical hemodynamic response function and its time derivative. The analyses were explicitly masked with a normalized within-brain mask of each subject derived by the segmentation of individual T1-images. Stimulus events were defined by the onsets and durations of corresponding stimulus presentations. Response events were modeled as a separate regressor, with onsets and durations according to the time the rating scale was present. If present, events with missing responses were modeled separately. Low-frequency signal drifts were filtered using a cutoff of 128 s. Following the first-level analyses, single subject contrasts were fed into the group analysis using a flexible factorial ANOVA (factors: condition and subject), employing a random-effects model. On the group level, differences between conditions and significant deviations from zero were assessed by linear contrasts on the second-level parameter estimates thresholded at $p<.05$ at the voxel level, FWE-corrected for multiple comparisons ($p_{\text{FWE-corr}}<.05$) and with a minimal cluster size of 30 voxels. Exceptionally, when reporting results from the analysis including both evaluation strength and arousal as parametric modulators a more liberal threshold of $p<.001$ at the voxel level, uncorrected for multiple comparisons ($p_{\text{uncorr}}<.001$) was applied as this analysis specifically served to confirm the significant effect of evaluation strength. Results were superimposed on the mean normalized T1-group image.

Three different statistical analyses were conducted. The first analysis focused on the SoE-effect by including both categorical and parametric neural responses to the stimuli into the model: (i) the categorical, general processing of verbal and nonverbal person information, respectively, disregarding its impact on subsequent evaluation (V and NV); and (ii) the parametric modulation of general processing by SoE (SoE-V and SoE-NV, defined as a difference from 0 on a 7-point rating scale: 0, 1, 2 or 3). For illustration purposes only, i.e., in order to provide plots for the better characterization of activation patterns across different SoE levels for significant brain regions, we also employed a categorical analysis, in which V and NV events with different absolute rating values were modeled as separate regressors. Here, eight events of interest were included in the analysis: V0, V1, V2, V3 and NV0, NV1, NV2, NV3 (see plots in Fig. 2A).

The second analysis aimed to demonstrate that differences in arousal ratings cannot explain the results of the parametric modulation. Here, the first analysis was repeated but with two linear parametric modulation factors: (i) first the arousal rating for each stimulus; and (ii) second the absolute valence rating for each stimulus. At the group level we again computed the SoE-V and SoE-NV contrasts, masked with the results from the main analysis. Because the second parametric modulation can only account for unique variance, which is not already accounted for by the first parametric modulation, this allows for ruling out the influence of the arousal of the stimuli on the impression strength effect.

The third analysis finally aimed to demonstrate that the SoE-effect was similar for positive and negative person information and included six events of interest: V−, V0, V+ and NV−, NV0, NV+. At the group level, valent, i.e. positively and negatively judged events (Val) were compared against neutrally rated events, separately for the verbal (Val-V) and nonverbal (Val-NV) domains (applied contrasts: 1 −2 1).

Results

The first analysis revealed distinct modulations of the general neural response by SoE for verbal and nonverbal stimuli, respectively. When judgments were based on nonverbal information, there was a linear signal increase in the bilateral amygdala with increasing SoE (see Fig. 2A and Table 2, SoE-NV). In contrast, when relying on verbal social information, increasing SoE correlated positively with the signal change in the left PC at the border to PCC (PC/PCC), the bilateral cuneus and cerebellum (see Fig. 2A and Table 2, SoE-V). These effects could mainly be replicated also in a direct comparison of SoE-V and SoE-NV, thereby resembling the plots in Fig. 2A. The contrast SoE-NV > SoE-V revealed a greater increase in the right hippocampus ($x=32$, $y=-10$, $z=-16$, $T=5.84$, $p_{\text{FWE-corr}}=.002$, cluster size = 48 voxels) and the right amygdala ($x=24$, $y=0$, $z=-20$, $T=5.39$, $p_{\text{FWE-corr}}=.009$, cluster size = 48 voxels, same cluster as the hippocampus). Conversely, the contrast SoE-V > SoE-NV revealed a greater increase in the right PC/PCC ($x=14$, $y=-60$, $z=34$, $T=4.97$, $p_{\text{FWE-corr}}=.039$, cluster size = 4 voxels) and the right cerebellum ($x=10$, $y=-50$, $z=-20$, $T=5.31$, $p_{\text{FWE-corr}}=.012$, cluster size = 12 voxels). However, the left amygdala and the bilateral cuneus did not exhibit a significantly different increase with increasing SoE across the two domains. Furthermore, contrasts targeting general responses to verbal and nonverbal stimuli irrespective of SoE revealed more widely distributed patterns of activation (V > NV, NV > V and conjunction between V and NV, V ∩ NV, see Fig. 3A and Table 3). Categorical comparison of verbal versus nonverbal stimuli revealed a network including the left STS, bilateral inferior parietal lobule (IPL), bilateral temporal pole, left PC/PCC, left dmPFC, left inferior frontal gyrus (IFG), left inferior temporal gyrus and left middle occipital gyrus. The opposite comparison of nonverbal versus verbal stimuli demonstrated involvement of the bilateral middle temporal gyrus, bilateral FFG, the right posterior STS extending into the IPL, the right middle frontal gyrus extending into the IFG, bilateral superior occipital gyrus and cuneus and the right thalamus. Finally, regions commonly activated by both verbal and nonverbal stimuli included the left FFG, bilateral calcarine sulci and inferior occipital gyri, the SMA, the left IPL, the bilateral anterior insula, the superior PC, the bilateral thalamus and the left IFG.

The second analysis included both arousal ratings and absolute valence ratings as parametric modulators in order to control for the effect of stimulus arousal. This analysis replicated the former SoE-effects by showing increasing BOLD signal in the bilateral amygdala with increasing SoE for the nonverbal domain ($x=-22$, $y=-10$, $z=-8$, $T=4.95$, $p_{\text{uncorr}}<.001$, cluster size = 284 voxels and $x=32$, $y=-12$, $z=-16$, $T=4.50$, $p_{\text{uncorr}}<.001$, cluster size = 125 voxels). Similarly, the equivalent contrast for verbal stimuli revealed the precuneus ($x=-10$, $y=-64$, $z=36$, $T=3.76$, $p_{\text{uncorr}}<.001$, cluster size = 15 voxels), the cerebellum ($x=6$, $y=-44$, $z=-24$, $T=4.99$, $p_{\text{uncorr}}<.001$, cluster size = 549 voxels) and the cuneus ($x=12$, $y=-78$, $z=12$, $T=4.50$, $p_{\text{uncorr}}<.001$, cluster size = 445 voxels). Thus, as the effects of the second parametric modulation in a model reveal only variance that had not been explained by the first parametric modulation, we can rule out that the effect of the increasing SoE could be explained by differences in stimulus-related arousal ratings.

Finally, the third analysis confirmed that the effect of increasing SoE does not reflect the influence of valence per se because the effect of valent versus neutral ratings was similar for both positive and negative social judgments. By comparing positive and negative against neutral judgments, we fully replicated the results from the first analysis (see Fig. 2B and Table 2, Val-V and Val-NV). In addition, direct comparisons between negative and positive verbal judgments (V− vs. V+ and V+ vs. V−) revealed no significant results within the whole brain, or when inclusively masked with SoE-V, even at a more liberal threshold ($p_{\text{uncorr}}<.001$). Similarly, comparing negative and positive nonverbal judgments (NV− vs. NV+ and NV+ vs. NV−) revealed no differences when inclusively masked with SoE-NV, even at a more liberal threshold ($p_{\text{uncorr}}<.001$). The comparison between negative and positive nonverbal stimuli within the whole brain, i.e. without masking, however, revealed a significantly stronger activation of the right superior temporal gyrus ($x=42$, $y=-30$, $z=12$, $T=5.77$, $p_{\text{FWE-corr}}=.001$, cluster size = 143 voxels) while no significant whole brain effect was found for the opposite contrast (NV+ vs. NV−), even at a more liberal threshold ($p_{\text{uncorr}}<.001$).

Discussion

The results of the present study show that neural regions specifically associated with increasing SoE during impression formation

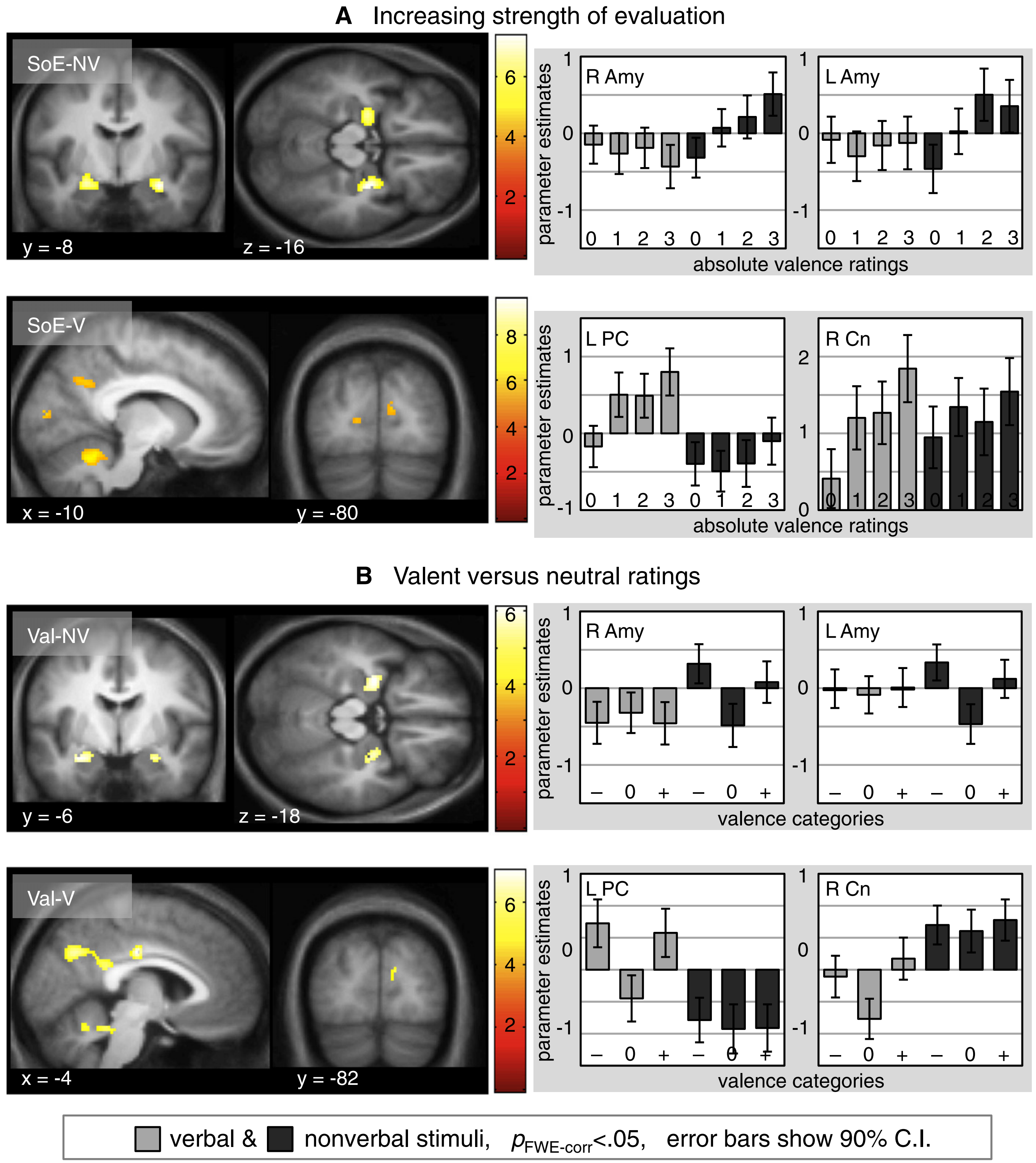

Fig. 2. Brain regions responsive to the outcome of subjective evaluative impressions based on a verbal or a nonverbal person information: A) Areas correlating with the increasing absolute valence ratings as a measure of the strength of evaluation (SoE), based on nonverbal (SoE-NV) and verbal (SoE-V) stimuli. Plots are derived by a supplementary analysis modeling events with different absolute ratings (0, 1, 2 or 3) as separate regressors; and B) Areas activating stronger during valent than neutral evaluations (Val), separately for nonverbal (Val-NV) and verbal (Val-V) stimuli, demonstrating a similar involvement for both positive and negative ratings.

differ depending upon the stimulus domain, i.e. between verbal and nonverbal stimuli. These effects were detectible for both positive and negative evaluations and even after controlling for subjectively rated arousal of the stimuli. Although pretests showed that verbal and nonverbal stimuli evoked comparable person evaluations at the behavioral level, increasing evaluation strength was associated with the bilateral amygdala for nonverbal stimuli and with the PC/PCC, bilateral cuneus and cerebellum for verbal stimuli. Hence, this finding indicates an involvement of qualitatively different cognitive processes during the evaluation of other persons dependent upon the stimulus domain.

Known to be a centerpiece of the affective system of the brain, the amygdala has been associated with diverse aspects of affective

Table 2
MNI coordinates of brain regions revealed by the parametric effect of increasing absolute evaluation ratings as a measure of the strength of evaluation (SoE) based on verbal (SoE-V) and nonverbal (SoE-NV) stimuli, and by the comparison between valent and neutral evaluation ratings based on verbal (Val-V) and nonverbal (Val-NV) stimuli.

Region	Cluster size (vox)	BA	Side	x	y	z	*t*
SoE-V							
Cerebellum	1018	–	R	10	−54	−20	9.54
			L	−6	−54	−22	7.22
PC/PCC	59	31	L	−12	−56	32	6.10
Cuneus	57	17/18	R	12	−76	14	5.67
	53	17	L	−8	−88	10	5.74
SoE-NV							
Amygdala	126	–	R	30	−8	−16	7.36
	110	–	L	−24	−8	−14	6.58
Val-V							
PCC	468	23	L	−10	−52	30	6.40
PC		31	L	−4	−66	34	6.13
Cerebellum	246	–	R	4	−46	−20	5.57
		–	L	−6	−40	−22	5.45
Middle cingulate gyrus	74	23	L	−4	−20	34	6.99
Lingual gyrus	55	17	R	12	−70	0	5.37
Cuneus	46	18	R	12	−82	20	5.35
Val-NV							
Amygdala	132	–	L	−30	−6	−18	6.12
	40	–	R	26	−6	−18	5.52

Reported are results that were significant at the voxel-level threshold $p<.05$, FWE-corrected for multiple comparisons, with a cluster size greater than 30 voxels; x, y, z, MNI coordinates of local maxima; BA, Brodmann area; PC, precuneus; PCC, posterior cingulate cortex; one voxel = 8 mm^3.

processing and learning (Zald, 2003). Providing further empirical support for its recruitment during the evaluation of other persons, our results also imply two more specific aspects: i) the amygdala was sensitive to changes in evaluation intensities, irrespective of valence; and ii) this response pattern was specific for nonverbal social information.

In concordance with the first point, the idea that the amygdala correlates with affective response intensities in a broad sense has recently received considerable empirical support. Overcoming the traditional conception that the amygdala is associated with negative valence only, neuroimaging studies (Anders et al., 2008; Sander and Scheich, 2001), as well as a quantitative meta-analysis (Sergerie et al., 2008) have demonstrated its recruitment for the processing of positive stimuli as well. Specifically regarding face evaluation, recent studies have shown that both highly trustworthy as well as highly untrustworthy faces activated the amygdala yielding a nonlinear, U-shaped response pattern (Said et al., 2009; Todorov et al., 2008). Similarly, the amygdala was engaged during judgments of absolute valences of emotional faces (Gerber et al., 2008). Furthermore, neuroimaging studies focusing specifically on interpersonal judgments have demonstrated that both positive and negative judgments recruit the amygdala when evaluating famous people (Cunningham et al., 2004, 2008) or when forming evaluative impressions of social others (Schiller et al., 2009). In the same line, the present study revealed that the more the nonverbal behavior displayed by the target person induced a pronounced impression, indexed by a greater SoE, the higher was the BOLD signal in the amygdala. Thus, our findings provide further support for the concept that the amygdala is especially sensitive to varying intensities of salient social information, irrespective of valence (Sander et al., 2003).

The second aspect with regard to the involvement of the amygdala in our study is that its increasing response with increasing SoE was specific for nonverbal stimuli. This result extends the findings by Schiller et al. (2009) by highlighting a closer association of the differential response in the amygdala with nonverbal social information in the context of increasingly extreme interpersonal evaluation. Taking into account its extensive projections to the occipital cortex, the amygdala is well positioned to modulate visual processing based on affective significance of the perceived input (Phelps and LeDoux, 2005; Vuilleumier and Pourtois, 2007). Consistently, converging evidence indicates its modulatory role in visual information processing, but not in recall and auditory induction methods of emotional responses (Phan et al., 2002). Furthermore, support for the specific sensitivity of the amygdala to nonverbal social cues has been provided by impairments in evaluating trustworthiness based on nonverbal, but not on verbal information in patients with amygdala lesions (Adolphs et al., 1998). Moreover, the recruitment of the amygdala for processing nonverbal stimuli has been shown to occur relatively independent of attentional resources or awareness, i.e., implicitly and automatically (Engell et al., 2007; Phelps and LeDoux, 2005; Phelps et al., 2000; Todorov and Engell, 2008; Winston et al., 2002). Although the essential role of the amygdala in the production of the social behavior has been questioned in prior studies on non-human primates, its role in detection of and reaction to especially threatening and hence significant stimuli

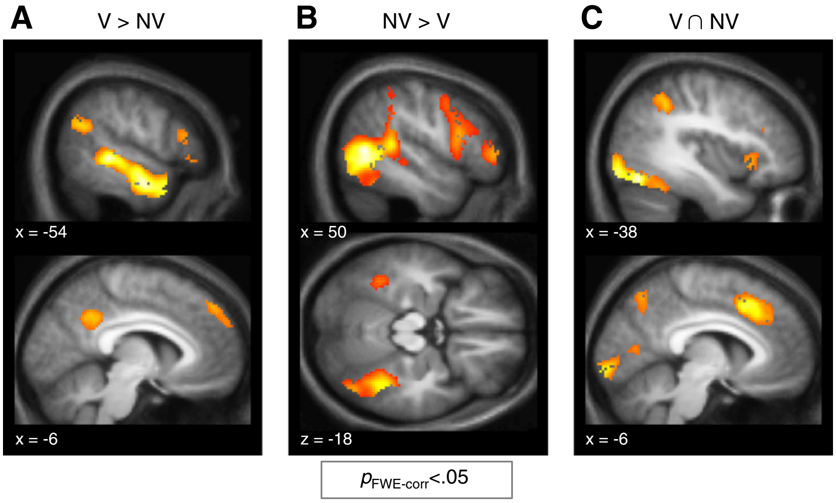

Fig. 3. Neuroimaging results relating to the general processing of verbal (V) and nonverbal (NV) person information, irrespective of subsequent ratings. A) Brain regions involved stronger in processing of verbal than nonverbal person information; B) Brain regions involved stronger in processing of nonverbal than verbal person information; C) Brain regions involved in processing of both verbal and nonverbal person information revealed by a conjunction.

Table 3
MNI coordinates of brain regions associated with the general processing of verbal (V) and nonverbal (NV) person information.

Region	Cluster size (vox)	BA	Side	x	y	z	T
V>NV							
Anterior STS	2001	21	L	−58	−6	−20	12.41
Posterior STS		22	L	−54	−36	0	11.66
Temporal pole		38	L	−48	16	−28	9.96
Angular gyrus	815	39	L	−44	−56	24	11.54
Middle occipital gyrus	377	18	L	−18	−90	−6	11.42
PC/PCC	298	31	L	−6	−52	36	7.00
dmPFC	235	9	L	−10	48	40	9.39
Middle frontal gyrus	190	6	L	−42	6	52	6.60
Middle temporal gyrus	148	21	R	58	4	−28	7.43
Temporal pole		21	R	56	10	−30	7.01
Inferior frontal gyrus	121	47	L	−50	30	−8	6.66
Inferior frontal gyrus	78	45	L	−52	24	18	6.26
		44	L	−52	16	28	4.93
Inferior temporal gyrus	67	37	L	−42	−62	−8	7.39
Angular gyrus	37	39	R	60	−58	26	7.10
NV>V							
Middle temporal gyrus, V5/MT+	3897	37	R	50	−62	6	17.06
Fusiform gyrus		37	R	42	−48	−18	12.26
Posterior STS		42	R	50	−40	12	11.87
Supramarginal gyrus		48	R	58	−38	26	10.63
Middle frontal gyrus	1770	10	R	46	42	4	11.04
Inferior frontal gyrus		44	R	48	14	20	9.78
Inferior frontal gyrus		45	R	44	32	16	7.94
Superior occipital gyrus	1404	17	L	−8	−98	12	17.61
Cuneus		18	R	10	−92	22	15.09
Middle temporal gyrus, V5/MT+	575	37	L	−48	−70	8	10.94
Fusiform gyrus	148	37	L	−40	−48	−18	7.42
Thalamus	76	–	R	18	−30	2	6.75
NV∩V							
Fusiform gyrus	3387	19	L	−40	−70	−16	12.80
Calcarine sulcus		17	R	16	−96	−6	12.33
		17	L	−6	−98	−6	8.50
Inferior occipital gyrus		19	R	34	−90	−12	12.11
		19	L	−38	−86	−10	10.55
SMA	666	6	L	−6	16	44	9.72
Inferior parietal lobule	382	7	L	−38	−48	44	7.36
Superior parietal lobule		7	L	−30	−60	46	5.45
Anterior insula	371	48	L	−30	20	−4	7.98
Precuneus	191	31	L	−6	−68	50	6.39
Inferior frontal gyrus	174	45	L	−50	30	28	7.63
Anterior insula	111	48	R	42	26	−8	6.05
Thalamus	68	–	L	−10	−12	6	5.54
Middle frontal gyrus	51	9	R	46	36	32	6.77
Thalamus	50	–	R	12	−8	4	6.11

Reported are results that were significant at the voxel-level threshold $p<.05$, FWE-corrected for multiple comparisons, with a cluster size greater than 30 voxels; x, y, z, MNI coordinates of local maxima; BA, Brodmann area; STS, superior temporal sulcus; PC, precuneus; PCC, posterior cingulate cortex; dmPFC, dorsomedial prefrontal cortex; SMA, supplementary motor area; one voxel = 8 mm^3.

within a social context has not been disproven (Amaral, 2003; Amaral et al., 2003). Given that understanding information conveyed by conspecifics' nonverbal signals occurs early in phylogenetic and ontogenetic development and plays a special role in adaptive social behavior, our findings may reflect an evolutionary shaped recruitment of the amygdala in the rapid detection and decoding of biologically and socially relevant information (Phelps and LeDoux, 2005; Sergerie et al., 2008).

Interestingly, the presentation of verbal and of neutral nonverbal stimuli was accompanied by deactivations in the amygdala, especially in the right hemisphere (see Fig. 2). Such right amygdala deactivations have been demonstrated already early on, by comparing active and passive conditions of different experiments, i.e. conditions where stimulus presentations were paired with demanding tasks versus with no task (Schulman et al., 1997). Moreover, those experiments that involved verbal processing tended to reveal larger deactivations in the right amygdala (Schulman et al., 1997). General task-induced deactivations are in accord with research demonstrating cognitive regulation of affective processing (Ochsner et al., 2002, 2004). Here, it has been shown that active cognitive computations were able to down-regulate affective processing and thereby decrease amygdala activity. Referring to neutral nonverbal stimuli in our study, the activity in the amygdala associated with detection of salient stimuli was possibly decreased simply because of the non-affective quality. Verbal stimuli, in contrast, may have induced a greater amount of high-level cognitive processing leading to a decreased activity of the amygdala as previously supposed by Freeman et al. (2010) for interpersonal judgments based on informative verbal stimuli. Additionally, paralleling patterns of activations have been demonstrated with other-race facial stimuli that increased the activation of the amygdala, while the perception of more neutral own-race facial stimuli resulted in slight deactivations (Lieberman et al., 2005). Furthermore, matching the race of the target face verbally and not via facial, i.e. nonverbal stimuli resulted in amygdala deactivations for both races (Lieberman et al., 2005).

On the other hand, our study highlights that when basing social judgments on verbal information, the BOLD signal increased in the PC/PCC, bilateral cuneus and cerebellum with increasing SoE. Thus, we replicated the findings by Schiller et al. (2009), who showed a specific involvement of the PCC in the evaluative component of impression formation and its parametric scaling with the SoE. Beyond this general functional characterization, we were able to demonstrate that the PC/PCC and its parametric activity changes are specifically associated with the processing of verbal stimuli. Consequently, our findings provide evidence for functional dissociations of 'social brain' regions based on the stimulus domain.

A similar dissociation has been demonstrated by a stronger involvement of the PCC in the processing of interpersonal judgments based on informative verbal material, while the amygdala was recruited when verbal stimuli were not informative and the judgment was reduced to an additionally presented face of the target person (Freeman et al., 2010). Our study extends these findings because it focuses specifically on the evaluative component of impression formation by making use of event-related subjective ratings instead of comparing two categories of person judgment irrespective of the subsequent outcome. Furthermore, due to the manipulation of both verbal and nonverbal stimuli in one experimental design, more valid conclusions about the influence and processing of the two domains can be derived from our study. Finally, in the present study both verbal and nonverbal information was individuated, i.e. related to idiosyncratic attributes and qualities of the target person indicated by social action descriptions and dynamic nonverbal communicative signals, respectively. Because nonverbal cues were displayed by the same virtual character, the content of social category knowledge extractable from the physical appearance such as gender, age, and race was identical across all nonverbal stimuli and could not serve as a basis for "superficial" decisions. This procedure implicates that not simply the degree of individuation but also the domain of social information determines the involvement of differential brain regions in evaluation of social others.

In general, the neurofunctional characterization of PCC has been more diverse than that of the amygdala. Social cognitive neuroscience research has assigned an important role to the PC/PCC in social inference including mentalizing, intention inference and impression formation (Lieberman, 2010) and in the interaction between episodic memory and the processing of emotionally salient words (Maddock, 1999; Maddock et al., 2003). Also, associations with the strength of evaluative judgments have been demonstrated by using verbal but not nonverbal stimuli (Maddock et al., 2003; Posner et al., 2009). At the same time, this region is characterized by its involvement in controlled, i.e., resource-limited processing in social cognitive tasks (Lieberman, 2010) and thus may also be associated with relatively deliberate processing. Thus, on a more speculative level, by revealing the association of PC/PCC with the verbal and of the amygdala with the nonverbal domain, we provide indirect evidence for hypotheses made by dual-process theories of social judgments (Evans, 2008; Lieberman et al., 2002). Here, it has been suggested that the two domains evoke automatic and controlled cognitive operations to different degrees that are associated with closely interacting but distinguishable neural substrates.

The cuneus comprising primary and secondary visual areas and the cerebellum were also differentially recruited by increasing evaluation strength based on verbal stimuli. The involvement of the visual cortex may be explained by the increased mental imagery of behaviors described in the more influential verbal stimuli (Lambert et al., 2002), possibly due to a higher selective attention toward a more diagnostic information (Kastner and Ungerleider, 2000). Similarly, the activation of the cerebellum was frequently reported for language- and emotion-related tasks (Stoodley and Schmahmann, 2009) and thus may represent a general increase of semantic and emotional processing of verbal stimuli with their increasing impact.

With regard to categorical comparisons of verbal and nonverbal stimuli, irrespective of the subsequent judgment, we could precisely replicate recent findings by Zaki et al. (2010) demonstrating domain-specific neural systems recruited when drawing inferences about emotional states of others based on either verbal or nonverbal social cues. A network related to mind state attribution including the dmPFC, the left PC/PCC and the bilateral temporal pole, as well as a left-lateralized network including inferior frontal, temporal and angular cortices associated with semantic processing (Price, 2000), were more strongly activated by verbal than by nonverbal stimuli. In contrast, nonverbal as compared to verbal stimuli more strongly engaged the right frontoparietal cortex corresponding to the putative human mirror neuron system (Rizzolatti and Craighero, 2004), as well as the right posterior STS, the bilateral FFG and the bilateral middle temporal gyrus including the area V5/MT+ involved in face and movement perception (Kanwisher and Yovel, 2006; Pelphrey et al., 2005; Wilms et al., 2005). Thus, our data support the notion that both the mentalizing and the mirror neuron system are involved in the general processing of social information about others, but obviously with different priorities for different domains (Zaki et al., 2010).

Critically, Zaki et al. (2010) also showed that when drawing inferences based on conflicting pairs of verbal and nonverbal information, activity in the right frontoparietal cortex and pSTS correlated with the relative reliance on nonverbal cues, whereas the activity in the left angular gyrus and mPFC correlated with the relative reliance on verbal cues. These results, however, must not be regarded as inconsistent with the domain-specific parametric modulation findings reported here because the two studies explored two different types of cognitive processes, namely person evaluation as opposed to inferences about emotional states of others. Moreover, the correlation of the activity in the amygdala with nonverbal and in the PC/PCC with verbal stimuli reported here was based on the strength of impression resulting from differentially salient unimodally presented information and not on the relative reliance on cues presented in a multimodal fashion.

Noteworthy, the activity in the dmPFC was not modulated by the increasing intensity of judgments for any domain, but was categorically stronger for processing verbal as compared to nonverbal person information. Thus, this finding provides additional evidence for the proposal that the dmPFC is not essential for the evaluative component of impression formation (Schiller et al., 2009). Rather, the dmPFC appears to be related to the general inferential processing of social information. Within the verbal domain, this inferential processing seems to occur regardless of information's diagnostic value as long as the instruction to form an impression is explicitly given evoking the continuous need to monitor social meanings (Mitchell et al., 2006). Similarly, in situations that specifically require an identification of non-observable mental states such as assessing deceptive intentions (Grezes et al., 2004a), false beliefs (Grezes et al., 2004b), reasons for actions (Spunt et al., 2011), moment-to-moment emotional states (Zaki et al., 2009) or social relations (Iacoboni et al., 2004) the dmPFC has been recruited by nonverbal social cues as well. However, without such an explicit need for sophisticated inferential computation, nonverbal stimuli may convey observable and expressive cues therefore engaging the dmPFC to a lesser extent (Spunt et al., 2011; Zaki et al., 2010).

With respect to limitations of the study, it is important to note that both the source of information and the semantic content differed between the two domains: While nonverbal stimuli implied a “self-report” with the target person presenting herself actively by the display of communicative expression and gesture, verbal stimuli were reputation-based and referred to descriptions of social actions. This approach was chosen because of its ecological validity as in everyday life we are frequently confronted with reputation-based verbal information about other persons' actions and nonverbal cues that are directly observed. Furthermore, verbal self-reports could induce the impression of target's self-projection that could influence the creditability of the given information. Although it is not indisputable that the differential SoE-effects for the two domains of information were neither influenced by the source of information nor by the semantic content, the comparison of the SoE-effect between the two domains as such is still valid because the SoE was computed separately within each domain. Furthermore, the differential recruitment of distant brain regions for the two domains is consistent with previous research in the related field as described above. However, in future studies the source of social information should be taken into account, for example, by using statements about controversial topics instead of action descriptions as verbal stimuli. Such statements would indicate a self-report comparable to the nonverbal domain thereby avoiding problems with creditability. The difference between the semantic contents referring to actions or opinions on the one hand and to expressive nonverbal signals on the other is more difficult to overcome, as these differences are inextricably constitutive of the verbal and nonverbal domain.

Another limitation is given by the use of female virtual characters only. This procedure was chosen in order to constrain the experimental design to the focus on the SoE effect by disregarding possible effects of the gender of the target person. However, it seems unlikely that similar effects would not occur also for male targets, because exactly such evaluation-related effects, but without a strict differentiation of the information domain, have been demonstrated in a study by Schiller et al. (2009), which used male target persons only and a gender-mixed sample of participants.

Furthermore, we only report the peaks of activation of isolated neural regions that do not provide any insights into the underlying neural networks. Further neuroimaging research should focus on methods targeting functional and anatomical connectivity in order to enrich our understanding of the neural mechanisms also on a network level of description. These methods could for example help to identify possible influences of increased attention to more informative and diagnostic social information resulting in more extreme judgments, which are not directly evident from the reported SoE effects.

Conclusions

The present study provides evidence for neurofunctional dissociation between the processing of verbal and nonverbal social information during interpersonal impression formation. Our results show that behaviorally similar social cognitive operations were driven by distinct neural networks when taking into account the kind of available information. While the influence of verbal stimuli on interpersonal judgments appears to rely on the PC/PCC, previously associated with mental state inferences, nonverbal social information shapes subsequent impression formation by the specific involvement of the amygdala, known to play a central role in automatic, affective processing. Instead of delineating these neurofunctional dissociations, however, in terms of independent dichotomies, it rather seems useful to characterize them as complementary parts of a complex interaction related to additional cognitive functions such as attention and memory. To explore these aspects further will be an important objective of future research. The question to what extent rapid, affective processes determine our social judgments and how this may relate to the presence of visual images has far reaching implications given the influence of impression formation on future expectations, decisions and behavior toward other persons. Due to the wide presence and increasing availability of visually transmitted information in today's media, this question is likely to take on even greater significance in the future.

Acknowledgments

We thank H. Kockler for helpful discussions and comments, E. Bannemer, R. Rosniak-Florath, A. Rühling and K. Wittenberg for assistance with data collection and T. Wetzel for technical support. This study was funded by the Federal Ministry of Education and Research (Germany) [Project “Other Minds”; grant number 01GP0802; KV].

References

Adolphs, R., Tranel, D., Damasio, A.R., 1998. The human amygdala in social judgment. Nature 393, 470–474.

Amaral, D.G., 2003. The amygdala, social behavior, and danger detection. Ann. N. Y. Acad. Sci. 1000, 337–347.

Amaral, D.G., Bauman, M.D., Schumann, C.M., 2003. The amygdala and autism: implications from non-human primate studies. Genes Brain Behav. 2, 295–302.

Ambady, N., Bernieri, F., Richeson, J., 2000. Towards a histology of social behavior: judgmental accuracy from thin slices of behavior. In: Zanna, M.P. (Ed.), Advances in Experimental Social Psychology, pp. 201–272.

Amodio, D.M., Frith, C.D., 2006. Meeting of minds: the medial frontal cortex and social cognition. Nat. Rev. Neurosci. 7, 268–277.

Anders, S., Eippert, F., Weiskopf, N., Veit, R., 2008. The human amygdala is sensitive to the valence of pictures and sounds irrespective of arousal: an fMRI study. Soc. Cogn. Affect. Neurosci. 3, 233–243.

Cunningham, W.A., Raye, C.L., Johnson, M.K., 2004. Implicit and explicit evaluation: FMRI correlates of valence, emotional intensity, and control in the processing of attitudes. J. Cogn. Neurosci. 16, 1717–1729.

Cunningham, W.A., Van Bavel, J.J., Johnsen, I.R., 2008. Affective flexibility: evaluative processing goals shape amygdala activity. Psychol. Sci. 19, 152–160.

Delgado, M.R., Frank, R.H., Phelps, E.A., 2005. Perceptions of moral character modulate the neural systems of reward during the trust game. Nat. Neurosci. 8, 1611–1618.

Engell, A.D., Haxby, J.V., Todorov, A., 2007. Implicit trustworthiness decisions: automatic coding of face properties in the human amygdala. J. Cogn. Neurosci. 19, 1508–1519.

Evans, J.S., 2008. Dual-processing accounts of reasoning, judgment, and social cognition. Annu. Rev. Psychol. 59, 255–278.

Freeman, J.B., Schiller, D., Rule, N.O., Ambady, N., 2010. The neural origins of superficial and individuated judgments about ingroup and outgroup members. Hum. Brain Mapp. 31, 150–159.

Gerber, A.J., Posner, J., Gorman, D., Colibazzi, T., Yu, S., Wang, Z., Kangarlu, A., Zhu, H., Russell, J., Peterson, B.S., 2008. An affective circumplex model of neural systems subserving valence, arousal, and cognitive overlay during the appraisal of emotional faces. Neuropsychologia 46, 2129–2139.

Grezes, J., Frith, C., Passingham, R.E., 2004a. Brain mechanisms for inferring deceit in the actions of others. J. Neurosci. 24, 5500–5505.

Grezes, J., Frith, C.D., Passingham, R.E., 2004b. Inferring false beliefs from the actions of oneself and others: an fMRI study. Neuroimage 21, 744–750.

Hariri, A.R., Tessitore, A., Mattay, V.S., Fera, F., Weinberger, D.R., 2002. The amygdala response to emotional stimuli: a comparison of faces and scenes. Neuroimage 17, 317–323.

Harris, L.T., Todorov, A., Fiske, S.T., 2005. Attributions on the brain: neuro-imaging dispositional inferences, beyond theory of mind. Neuroimage 28, 763–769.

Iacoboni, M., Lieberman, M.D., Knowlton, B.J., Molnar-Szakacs, I., Moritz, M., Throop, C.J., Fiske, A.P., 2004. Watching social interactions produces dorsomedial prefrontal and medial parietal BOLD fMRI signal increases compared to a resting baseline. Neuroimage 21, 1167–1173.

Kanwisher, N., Yovel, G., 2006. The fusiform face area: a cortical region specialized for the perception of faces. Philos. Trans. R. Soc. Lond. B Biol. Sci. 361, 2109–2128.

Kastner, S., Ungerleider, L.G., 2000. Mechanisms of visual attention in the human cortex. Annu. Rev. Neurosci. 23, 315–341.

Kraemer, N.C., 2008. Nonverbal communication. In: Blascovich, J.J., Hartel, C.R. (Eds.), Human Behavior in Military Contexts. National Academic Press, Washington, pp. 150–188.

Kuzmanovic, B., Schilbach, L., Lehnhardt, F.-G., Bente, G., Vogeley, K., 2011. A matter of words: impact of verbal and nonverbal information on impression formation in high-functioning autism. Res. Autism Spectr. Disord. 5, 604–613.

Lambert, S., Sampaio, E., Scheiber, C., Mauss, Y., 2002. Neural substrates of animal mental imagery: calcarine sulcus and dorsal pathway involvement—an fMRI study. Brain Res. 924, 176–183.

Lieberman, M.D., 2010. Social cognitive neuroscience. In: Fiske, S.T., Gilbert, D.T., Lindzey, G. (Eds.), Handbook of Social Psychology. McGraw Hill, New York, pp. 143–193.

Lieberman, M.D., Gaunt, R., Gilbert, D.T., Trope, Y., 2002. Reflection and reflexion: a social cognitive neuroscience approach to attributional inference. Adv. Exp. Soc. Psychol. 34, 199–249.

Lieberman, M.D., Hariri, A., Jarcho, J.M., Eisenberger, N.I., Bookheimer, S.Y., 2005. An fMRI investigation of race-related amygdala activity in African-American and Caucasian-American individuals. Nat. Neurosci. 8, 720–722.

Maddock, R.J., 1999. The retrosplenial cortex and emotion: new insights from functional neuroimaging of the human brain. Trends Neurosci. 22, 310–316.

Maddock, R.J., Garrett, A.S., Buonocore, M.H., 2003. Posterior cingulate cortex activation by emotional words: fMRI evidence from a valence decision task. Hum. Brain Mapp. 18, 30–41.

Mitchell, J.P., Heatherton, T.F., Macrae, C.N., 2002. Distinct neural systems subserve person and object knowledge. Proc. Natl. Acad. Sci. U. S. A. 99, 15238–15243.

Mitchell, J.P., Neil Macrae, C., Banaji, M.R., 2005. Forming impressions of people versus inanimate objects: social-cognitive processing in the medial prefrontal cortex. Neuroimage 26, 251–257.

Mitchell, J.P., Cloutier, J., Banaji, M.R., Macrae, C.N., 2006. Medial prefrontal dissociations during processing of trait diagnostic and nondiagnostic person information. Soc. Cogn. Affect. Neurosci. 1, 49–55.

Ochsner, K.N., Bunge, S.A., Gross, J.J., Gabrieli, J.D., 2002. Rethinking feelings: an FMRI study of the cognitive regulation of emotion. J. Cogn. Neurosci. 14, 1215–1229.

Ochsner, K.N., Ray, R.D., Cooper, J.C., Robertson, E.R., Chopra, S., Gabrieli, J.D., Gross, J.J., 2004. For better or for worse: neural systems supporting the cognitive down- and up-regulation of negative emotion. Neuroimage 23, 483–499.

Ochsner, K.N., Beer, J.S., Robertson, E.R., Cooper, J.C., Gabrieli, J.D., Kihsltrom, J.F., D'Esposito, M., 2005. The neural correlates of direct and reflected self-knowledge. Neuroimage 28, 797–814.

Pelphrey, K.A., Morris, J.P., Michelich, C.R., Allison, T., McCarthy, G., 2005. Functional anatomy of biological motion perception in posterior temporal cortex: an FMRI study of eye, mouth and hand movements. Cereb. Cortex 15, 1866–1876.

Phan, K.L., Wager, T., Taylor, S.F., Liberzon, I., 2002. Functional neuroanatomy of emotion: a meta-analysis of emotion activation studies in PET and fMRI. Neuroimage 16, 331–348.

Phelps, E.A., LeDoux, J.E., 2005. Contributions of the amygdala to emotion processing: from animal models to human behavior. Neuron 48, 175–187.

Phelps, E.A., O'Connor, K.J., Cunningham, W.A., Funayama, E.S., Gatenby, J.C., Gore, J.C., Banaji, M.R., 2000. Performance on indirect measures of race evaluation predicts amygdala activation. J. Cogn. Neurosci. 12, 729–738.

Posner, J., Russell, J.A., Gerber, A., Gorman, D., Colibazzi, T., Yu, S., Wang, Z., Kangarlu, A., Zhu, H., Peterson, B.S., 2009. The neurophysiological bases of emotion: an fMRI study of the affective circumplex using emotion-denoting words. Hum. Brain Mapp. 30, 883–895.

Price, C.J., 2000. The anatomy of language: contributions from functional neuroimaging. J. Anat. 197 (Pt. 3), 335–359.

Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. Annu. Rev. Neurosci. 27, 169–192.

Said, C.P., Baron, S.G., Todorov, A., 2009. Nonlinear amygdala response to face trustworthiness: contributions of high and low spatial frequency information. J. Cogn. Neurosci. 21, 519–528.

Sander, K., Scheich, H., 2001. Auditory perception of laughing and crying activates human amygdala regardless of attentional state. Brain Res. Cogn. Brain Res. 12, 181–198.

Sander, D., Grafman, J., Zalla, T., 2003. The human amygdala: an evolved system for relevance detection. Rev. Neurosci. 14, 303–316.

Schiller, D., Freeman, J.B., Mitchell, J.P., Uleman, J.S., Phelps, E.A., 2009. A neural mechanism of first impressions. Nat. Neurosci. 12, 508–514.

Schulman, G.L., Fiez, J.A., Corbetta, M., Buckner, R.L., Miezin, F.M., Raichle, M.E., Petersen, S.E., 1997. Common blood flow changes across visual tasks: II. Decreases in cerebral cortex. J. Cogn. Neurosci. 9, 648–663.

Serences, J.T., 2004. A comparison of methods for characterizing the event-related BOLD timeseries in rapid fMRI. Neuroimage 21, 1690–1700.

Sergerie, K., Chochol, C., Armony, J.L., 2008. The role of the amygdala in emotional processing: a quantitative meta-analysis of functional neuroimaging studies. Neurosci. Biobehav. Rev. 32, 811–830.

Spunt, R.P., Satpute, A.B., Lieberman, M.D., 2011. Identifying the what, why, and how of an observed action: an fMRI study of mentalizing and mechanizing during action observation. J. Cogn. Neurosci. 23, 63–74.

Stoodley, C.J., Schmahmann, J.D., 2009. Functional topography in the human cerebellum: a meta-analysis of neuroimaging studies. Neuroimage 44, 489–501.

Sugiura, M., Gotoh, R., Okada, K., Yamaguchi, K., Itoh, M., Fukuda, H., Kawashima, R., 2004. Target dependency of brain mechanism involved in dispositional inference: a PET study. Neuroimage 21, 1377–1386.

Todorov, A., 2008. Evaluating faces on trustworthiness: an extension of systems for recognition of emotions signaling approach/avoidance behaviors. Ann. N. Y. Acad. Sci. 1124, 208–224.

Todorov, A., Engell, A.D., 2008. The role of the amygdala in implicit evaluation of emotionally neutral faces. Soc. Cogn. Affect. Neurosci. 3, 303–312.

Todorov, A., Baron, S.G., Oosterhof, N.N., 2008. Evaluating face trustworthiness: a model based approach. Soc. Cogn. Affect. Neurosci. 3, 119–127.

Uleman, J.S., Adil Saribay, S., Gonzalez, C.M., 2008. Spontaneous inferences, implicit impressions, and implicit theories. Annu. Rev. Psychol. 59, 329–360.

Vuilleumier, P., Pourtois, G., 2007. Distributed and interactive brain mechanisms during emotion face perception: evidence from functional neuroimaging. Neuropsychologia 45, 174–194.

Watzlawick, P., Bavelas, J.H., Jackson, D.D., 1967. Pragmatics of Human Communication: a Study of Interactional Patterns, Pathologies, and Paradoxes. Norton, New York.

Wilms, M., Eickhoff, S.B., Specht, K., Amunts, K., Shah, N.J., Malikovic, A., Fink, G.R., 2005. Human V5/MT+: comparison of functional and cytoarchitectonic data. Anat. Embryol. (Berl.) 210, 485–495.

Winston, J.S., Strange, B.A., O'Doherty, J., Dolan, R.J., 2002. Automatic and intentional brain responses during evaluation of trustworthiness of faces. Nat. Neurosci. 5, 277–283.

Zaki, J., Weber, J., Bolger, N., Ochsner, K., 2009. The neural bases of empathic accuracy. Proc. Natl. Acad. Sci. U. S. A. 106, 11382–11387.

Zaki, J., Hennigan, K., Weber, J., Ochsner, K.N., 2010. Social cognitive conflict resolution: contributions of domain-general and domain-specific neural systems. J. Neurosci. 30, 8481–8488.

Zald, D.H., 2003. The human amygdala and the emotional evaluation of sensory stimuli. Brain Res. Brain Res. Rev. 41, 88–123.

Zysset, S., Huber, O., Ferstl, E., von Cramon, D.Y., 2002. The anterior frontomedian cortex and evaluative judgment: an fMRI study. Neuroimage 15, 983–991.

NeuroImage 53 (2010) 291–302

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Animated brain: A functional neuroimaging study on animacy experience

Natacha S. Santos [a,*], B. Kuzmanovic [a], N. David [b], A. Rotarska-Jagiela [a], S.B. Eickhoff [c], J.N. Shah [d], G.R. Fink [d,e], G. Bente [f], K. Vogeley [a]

[a] *Department of Psychiatry, University of Cologne, Germany*
[b] *Institute of Neurophysiology and Pathophysiology, Center of Experimental Medicine, University Medical Center Hamburg-Eppendorf, Germany*
[c] *Department of Psychiatry and Psychotherapy, University of Aachen, Germany*
[d] *Institute of Neurosciences and Medicine (INM), Research Center Juelich, Germany*
[e] *Department of Neurology, University of Cologne, Germany*
[f] *Department of Social and Media Psychology, University of Cologne, Germany*

ARTICLE INFO

Article history:
Received 26 November 2009
Revised 21 May 2010
Accepted 27 May 2010
Available online 4 June 2010

Keywords:
Animacy
Insula
Mentalizing
Mirror neuron system (MNS)
Social neural network (SNN)
Superior temporal sulcus
Orbitofrontal cortex
Ventromedial prefrontal cortex

ABSTRACT

Previous research used animated geometric figures to investigate social cognitive processes involved in ascribing mental states to others (e.g. mentalizing). The relationship between animacy perception and brain areas commonly involved in social cognition, as well as the influence of particular motion patterns on animacy experience, however, remains to be further elucidated. We used a recently introduced paradigm for the systematic variation of motion properties, and employed functional magnetic resonance imaging to identify the neural mechanisms underlying animacy experience. Based on individual ratings of increased animacy experience the following brain regions of the "social neural network" (SNN), known to be involved in social cognitive processes, were recruited: insula, superior temporal gyrus, fusiform gyrus, parahippocampal gyrus and the ventromedial prefrontal cortex bilaterally. Decreased animacy experience was associated with increased neural activity in the inferior parietal and inferior frontal gyrus, key constituents of the human "mirror neuron system" (hMNS). These findings were corroborated when analyses were based on movement patterns alone, irrespective of subjective experience. Additionally to the areas found for increased animacy experience, an increase in interactive movements elicited activity in the amygdala and the temporal pole. In conclusion, the results suggest that the hMNS is recruited during a low-level stage of animacy judgment representing a basic disposition to detect the salience of movements, whereas the SNN appears to be a high-level processing component serving evaluation in social and mental inference.

Introduction

Humans like most other animals equipped with visual senses are very sensitive to detect biological motion in their environment. The attribution of liveliness in humans leads to inferences about the perceived intentions, emotions and social relations of others often subsumed under the headings of "mentalizing" and "Theory of Mind" (ToM). These social cognitive capacities are assumed to be a uniquely human capacity (Tomasello et al., 2005). Phenomenologically, biological motion constitutes a complex perceptual input conveying information about physical properties of the moving object (e.g. anatomy, size, and weight), its interrelation to the physical and social environment (e.g. gravity, responses to barriers, approach and avoidance), its behavioural capacities (e.g. sophistication and efficiency in performing motor tasks) and potentially also about psychological processes or mental states (e.g. thoughts, intentions, emotions, etc.). Previous research could amply demonstrate that movement properties as attached to graphically reduced object representations, such as point-light-walkers, are sufficient to perceive an object as alive, to extract various types of information (e.g. the action and identity of the agent) and to make meaningful inferences (Blake and Shiffrar, 2007; Johansson, 1973).

Research on the experience of animacy has put forward the notion that different variations of movement influence our ability to attribute mental states to moving objects independently of their structure or form (Abell et al., 2000; Barrett et al., 2005; Heider and Simmel, 1944; Rochat et al., 1997; Santos et al., 2008; Tremoulet and Feldman, 2006). This 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. Thereby, the perception of animacy requires a type of motion able to trigger the impression that an entity is alive, and that it also possesses some degree of "mind", whether very simple goal-directed (e.g. moving to reach an apple) or complex mental states like mentalizing. Thus, it is our interpretation of other entities as having a mind that ultimately leads to a perception of animacy (Santos et al., 2008; Tremoulet and

---

* Corresponding author. Department of Psychiatry, University of Cologne, Kerpenerstr. 62, 50924 Cologne, Germany.
E-mail address: natachasantos@gmail.com (N.S. Santos).

1053-8119/$ – see front matter © 2010 Elsevier Inc. All rights reserved.
doi:10.1016/j.neuroimage.2010.05.080

Feldman, 2006). Movement features contributing to animacy perception include self-propelled motion, such as initiation of movement without an external cause (Leslie, 1984; Stewart, 1984), motion contingency (spatial and temporal synchrony) between objects (Bassili, 1976; Blakemore et al., 2003; Johnson, 2003; Johnson et al., 2001), and responsiveness to the motion by the environment (Abell et al., 2000; Blakemore et al., 2003, 2001; Castelli et al., 2000; Leslie, 1984; Michotte, 1946; Rochat et al., 1997; Santos et al., 2008; Schlottmann and Surian, 1999; Schultz et al., 2005; Springer et al., 1996; Tremoulet and Feldman, 2006). In our own study, participants experienced an increase in animacy perception whenever the animations displayed a combination of movement cues (e.g. break of a smooth movement trajectory, approach of one object to the other, and responsiveness from the addressed object to the actively moving object) (Santos et al., 2008).

Social cognition involves the cognitive perceptual and conceptual processes, which helps us make sense of our social world. The amygdala, the orbital frontal cortex and the temporal cortex are considered part of the social brain since its original description by Brothers in 1990 (Brothers, 1990). Subsequently, a vast number of neuroimaging studies have contributed to our present knowledge of how social information is processed at the neural level. Although some debate exist to which brain areas constitute the what is now called "social neural network" (SNN), across different social researchers these include the ventromedial prefrontal cortex (vmPFC) (Adolphs, 2009; Amodio and Frith, 2006; Beer and Ochsner, 2006; Bifulco et al., 2006; Blakemore, 2008; Brothers, 1990; Frith, 2007; Skuse and Gallagher, 2009; Van Overwalle, 2009), the superior temporal sulcus (STS) and gyrus (STG) (Adolphs, 2003; Amodio and Frith, 2006; Beer and Ochsner, 2006; Blakemore, 2008; Frith, 2007; Gallese et al., 2004; Van Overwalle, 2009), the insula (Adolphs, 1999; Blakemore, 2008; Frith and Frith, 2006), the amygdala (Adolphs, 1999, 2001, 2003; Blakemore, 2008; Brothers, 1990; Frith, 2007; Pinkham et al., 2008; Skuse and Gallagher, 2009), the fusiform gyrus (FG) (Adolphs, 2003; Beer and Ochsner, 2006; Blakemore, 2008), and the anterior temporal poles (TP) (Amodio and Frith, 2006; Blakemore, 2008; Frith, 2007; Pinkham et al., 2003). Some of these brain areas are typically implicated in mentalizing processes, essential for social cognition, constituting the ToM neural network: the medial prefrontal cortex, the STS/STG, and the precuneus (Frith and Frith, 2003; Gallagher and Frith, 2003; Gobbini et al., 2007; Van Overwalle and Baetens, 2009). Observing animated movement patterns, independently of the characters shape and form, can elicit increased neural activation in brain areas that are part of the SNN (Blakemore et al., 2003; Castelli et al., 2002; Castelli et al., 2000; Chaminade et al., 2007; Gobbini et al., 2007; Martin and Weisberg, 2003; Schultz et al., 2005, 2004, 2003; Tavares et al., 2008; Wheatley et al., 2007), and in areas that are specifically related to the ToM network. Using animations similar to those developed by Heider and Simmel (1944), Castelli et al. (2000) in a PET study found increased activations in vmPFC and basal temporal regions (fusiform gyrus and TP), when comparing animations eliciting ToM with random motion animations (Castelli et al., 2000). More recently, it was demonstrated an increased activity in the anterior cingulate cortex (ACC), as part of the medial prefrontal cortex, both under the presentation of ToM stories and ToM animations, but not during the observation of simple point-light displays of human motion (Gobbini et al., 2007). In accordance with others (Walter et al., 2004) the authors proposed a crucial role of the ACC in the representation of the social intentions of actions. The STS has also been implicated in processing the kinematics of geometrical figures, in particular related to those properties that are strongly tied to animacy perception such as goal-directed motion (Schultz et al., 2004), contingency between objects (Blakemore et al., 2003) and interactivity (Schultz et al., 2005).

While most neuroimaging studies that have used animated stimuli aimed at evoking ToM in human subjects (Campbell et al., 2006; Castelli et al., 2002; Castelli et al., 2000; Gobbini et al., 2007; Horan et al., 2009; Kana et al., 2009; Russell et al., 2006; Salter et al., 2008), only few studies focused on the neural correlates of animacy experience (Wheatley et al., 2007) and the relation between animacy and social cognition (Martin and Weisberg, 2003; Tavares et al., 2008). Focusing on neural correlates of animacy perception, Wheatley et al. (2007) compared animations of the same object moving with different backgrounds in the absence of any social content, which either lead to interpretations of animacy (e.g. "ice-skating") or of inanimacy (e.g. "spinning-top") (Wheatley et al., 2007). The interpretation of the same motion as animated (depending on background) was sufficient to elicit activations throughout the SNN. Similarly, Tavares et al. (2008) manipulated the attended aspect of two animated circles by instructing the subjects to focus on either the social interaction between them or motion properties such as speed (Tavares et al., 2008). Viewing animations while attending to social cues in contrast to motion properties activated areas previously linked to the SNN, namely the fusiform gyrus, the STS, and the amygdala.

The present study investigates the neural correlates of animacy experience and the parallels between animacy experience and the SNN. In addition, we were interested in identifying movement patterns that strongly influence increases in animacy experience at the neural level. We employed a previously developed paradigm aiming at inducing an increase in animacy experience, which was confirmed behaviourally in our first previous study (Santos et al., 2008). The movies we used range from movies that could clearly be judged as animated to movies that could clearly be judged as least animated, while the majority was more ambiguous. This ambiguity, we believe, was fundamental to induce subjective ratings, so that judgments depended entirely on the individual subjective experience of animacy. The design involves systematic variations of motion parameters shown to successfully induce and parametrically vary the experience of animacy including the degree of interaction between two objects (e.g. approach and responsiveness) (Dittrich and Lea, 1994; Santos et al., 2008; Schultz et al., 2005) and the time delay one object spent in the vicinity of another object (Santos et al., 2008). Subjects saw three-dimensional (3D) animations of two spheres displaying different types of movement sequences, and were instructed to judge each animation as (i) physical, (ii) rather physical, (iii) rather personal or (iv) personal. This allowed a parametric analysis of fMRI data according to increased vs. decreased animacy, based on subjective experience and physical properties of the stimuli.

Materials and methods

Subjects

Fifteen male subjects (mean age = 26.59 ± 3.94) without any past medical history with respect to psychiatric or neurological diseases participated in the study. All had normal or corrected-to-normal vision. Written informed consent was obtained and all participants were informed of the necessary safety precautions involving fMRI experiments prior to the scanning session. The study was approved by the local ethics committee of the Medical Faculty of the University of Cologne, Germany.

Stimuli and design

The stimuli consisted of 104 animations showing two 3D-spheres moving on a black background. The basic scenery comprised one sphere crossing the setting horizontally in the background (sphere1) and one static sphere in the foreground (sphere2). The following stimulus parameters were systematically varied: 1) the time sphere1 spent in the center of the screen: 0 (without break), 100, 200, 400, 600, 800 and 1000 ms ("time delay"); 2) whether the moving sphere1 did approach sphere2 or not ("approach"); 3) whether sphere2 moved toward the moving sphere1 (“responsiveness”); 4) the vertical perspective view of the scene: 30° or 60° (“perspective”); 5) whether the moving sphere1 crossed from left to right or vice versa (“direction”). Approach and responsiveness were varied in a 2×2 factorial design (no approach + no responsiveness; no approach + responsiveness; approach + no responsiveness; approach + responsiveness) and each of the factorial combinations was designed in six time delay variations (from 100 to 1000 ms), two vertical view perspectives (30° or 60°) and two movement directions (right–left, left–right). Additionally, animations without approach (no approach + no responsiveness; no approach + responsiveness) were also presented without break (time delay = 0 ms), resulting in 26 stimuli. Animations with approach always had a break (time delay > 0 ms) to ensure “plausibility of the behaviour” and thus ecological validity. Finally, each of these stimuli was repeatedly presented in both perspectives and in both directions. This resulted in a parametric variation of physical properties of the stimulus material. All animations were created using “3D Studio Max” software (version 7, Autodesk, Montreal, Canada). The participants' task was to rate the animacy of each animation according to a four-step scale (animacy judgements: “physical”, “rather physical”, “rather personal” and “personal”) by pressing the respective buttons on an MRI-compatible response device (Lumitouch, Lightwave Medical Industries, CST Coldswitch Technologies). In order to facilitate the understanding of the rating scale, we have defined the rating scale extremes as opposite terms, i.e., “physical” vs. “personal”, instead of using a more abstract labelling, i.e., “least animated” vs. “very animated”. Due to the continuous systematic generation of stimuli, the changes in the amount of animacy-related features of movement patterns and thus in the subjective animacy perception are to be defined as representing the dimension of animacy, where increases and decreases can be determined. Subjects were instructed to answer as soon as they felt confident in their judgment, i.e., did not have to wait until the end of the animation. Between the video sequences a small white fixation cross was presented in the center of the screen for 2–4 s, to allow the estimation of event-related responses (Josephs and Henson, 1999). The presentation of the stimuli was divided into four sessions of 52 animations each with a total measurement time of approximately 20 min. All animations were presented during the first two sessions and repeated during the last two sessions to increase measurement reliability and statistical power. In order to prevent order effects, all trials were randomly presented within each session and for each participant. Instructions and six example trials were provided to the participants prior to the scanning procedure.

fMRI data acquisition

A 3 T whole body system (Siemens TRIO), equipped with a standard head coil and a custom-built head holder for movement reduction was used to acquire high-resolution T1-weighted structural images (TR = 2500 ms, TE = 3.93 ms, voxel size: 1×1×1 mm, 256 mm FOV, 256×256 matrix) and T2-weighted EPI images (TR = 2500 ms, TE = 30 ms, 40 axial slices aligned parallel to the AC–PC plane, flip angle = 90°, voxel size: 3.1×3.1×3 mm, 200 mm FOV, 64×64 matrix, 147 volumes per session). Three additional volumes were collected and discarded at the beginning of each session to allow for magnetic saturation.

The fMRI protocol was an event-related design with a pseudorandomized jitter of 2000 to 4000 ms (in steps of 100 ms) between trials. Pseudo-randomisation of inter-event intervals ensured random sub-sampling of the neural response relative to the onset of the different event-types. All stimuli were presented on a screen located behind the participants' head and reflected to his field of vision via a mirror mounted on the head coil. Programming of the experiment and presentation of the stimuli were done using the “Presentation” software (Version 9.90, Neurobehavioral Systems).

Data analysis

Behavioural data

The effect of factors of interest approach, responsiveness and time delay on subjects' ratings was tested by a three-way repeated measures analysis of variance (ANOVA) using SPSS (SPSS Statistics 17.0). Only the levels of time delay higher than 0 (six levels between 100 and 1000 ms) were included in the analysis as the time delay level of 0 was realized only for the sequences without approach (see Stimuli and design).

Preprocessing of fMRI data

Image processing and analysis of fMRI data were performed using the statistical parametric mapping software (SPM5) (Wellcome Trust Centre for Neuroimaging; www.fil.ion.ucl.ac.uk/spm). All functional images for each subject were corrected for slice acquisition delays and spatially realigned to correct for head movement during the scanning procedure. Each structural MRI was co-registered to the subject's mean realigned functional image. Images were then normalized into a standard stereotactic space using the Montreal Neurological Institute (MNI) template. Functional images were spatially smoothed with an isotropic Gaussian filter (8 mm full width at half maximum) to account for residual interindividual differences.

Statistical analyses of fMRI data

Two sets of analyses of the imaging data were performed. In all analyses the data were analyzed using a General Linear Model as implemented in SPM5. Furthermore, effects of interest were modelled using a boxcar reference vector convolved with the canonical hemodynamic response function (hrf) and its first-order time derivative. The events of interest covered the last second of the stimulus movies, thereby focusing on the time window where the events became meaningful (corresponding to the spheres movements). A 128 s temporal high-pass filter was applied to account for low-frequency drifts. Spatial realignment parameters were included as confounds to exclude movement-related variance from the image time series. The single subject contrasts were fed into the second level group analyses using a flexible factorial ANOVA (factors: condition and subject), employing a random-effects model (Penny et al., 2003). At the group level, brain regions with increased neural activation are reported throughout at a cluster-level threshold of $p<0.05$, FWE corrected for multiple comparisons and a voxel-level threshold of $p<0.0005$, uncorrected for multiple comparisons (Friston et al., 1996). For the first set of response-related analyses we used a more liberal threshold at the voxel level ($p<0.005$ at the voxel level, uncorrected). All anatomical regions and denominations are reported according to a standard brain atlas (Duvernoy, 1999) and the Anatomy toolbox implemented in SPM5 (Eickhoff et al., 2007; Eickhoff et al., 2005). Reported coordinates refer to maximum values in a given cluster according to the standard MNI-template. For the purpose of additional anatomical precision, group contrasts were overlaid on a surface based representation of the MNI canonical brain using the SPM surfrend toolbox (written by I.Kahn; http://spmsurfrend.sourceforge.net). The surfaces were then rendered using NeuroLens (written by Dr. R. Hoge; http://neurolens.org).

Statistical analyses based on animacy experience (subjective ratings)

In the first set of analyses we used subjects' individual ratings of the movies in order to identify brain regions with increased neural activation, as a function of an increased or decreased degree of subjectively perceived animacy. The effect of subject's ratings was modelled as a linear parametric modulation of the hemodynamic response to the movies by the corresponding rating. For each single movie event both (i) the onset was defined within the regressor representing the last second of the stimulus (onset = endpoint minus 1 s); and (ii) the effect of subjective animacy experience defined by the corresponding rating to each movie (values referred to the subjective ratings made on a 4-step rating scale). At the group level, two *t*-contrasts were computed: (i) the positive effect of responses, that is, brain regions with increased neural activation corresponding to increases in animacy ratings; and (ii) the negative effect of responses, that is, brain regions with increased neural activation corresponding to decreases in animacy ratings. Additionally, in a supplementary analysis, we employed a categorical design where movies that were rated with 1 (physical), 2 (rather physical), 3 (rather personal) or 4 (personal) were modelled on separate regressors. The four rating-related contrasts were included in the group level analysis and an *F*-contrast was computed for the effect across all four response conditions in order to obtain plots with contrast estimates for each rating step at the local maxima from the first analysis.

Statistical analyses based on movement patterns (physical properties of the stimulus material)

In the second set of analyses we focused on the physical movement patterns that showed significant effects on animacy ratings (see “Results of behavioural data”), namely approach and responsiveness (as described in the “Stimuli and design” section). At the single subject level of the combined analysis based on the 2 × 2 design of the factors approach and responsiveness, we were able to identify brain regions with increased neural activation as a function of increasing interactive movements between the spheres, simulating social interaction. For the linear parametric modulation of the hemodynamic response to the movies we used the following codes corresponding to four types of movement patterns: (i) no approach + no responsiveness (coded with 1); (ii) no approach + responsiveness (coded with 2); (iii) approach + no responsiveness (coded with 3); (iv) approach + responsiveness (coded with 4). At the group level, the following two *t*-contrasts were computed: (i) the positive effect of movement patterns, that is, brain regions with increased neural activation corresponding to an increase in interactive movements; and (ii) the negative effect of movement patterns, that is, brain regions with increased neural activation corresponding to a decrease in interactive movements. Additionally, in a supplementary analysis, we employed a categorical design where movies with different movement pattern codes were modelled on separate regressors. As in the first set of analyses, the resulting *F*-contrast was used to obtain plots with contrast estimates for the local maxima from the analysis with parametric modulation of movement patterns.

Results

Behavioural data

Descriptive statistics revealed that subjects rated 14.4% of the animations as “physical”, 27.8% as “rather physical”, 34% as “rather personal”, and 24% as “personal”. The ANOVA revealed that there were significant main effects of approach ($F(1,14) = 82.142$, $p < 0.001$, $r = 0.924$) and responsiveness ($F(1,14) = 10.919$, $p < 0.05$, $r = 0.661$) indicating more personal ratings for sequences with approach ($M = 3.18$, $\mathrm{SE} = 0.105$) than without approach ($M = 2.342$, $\mathrm{SE} = 0.112$) as well as more personal ratings for sequences with responsiveness ($M = 3.00$, $\mathrm{SE} = 0.135$) than without responsiveness ($M = 2.52$, $\mathrm{SE} = 0.107$). Neither the main effect of time delay ($F(5,70) = 1.079$, $p = 0.380$) nor any of the possible interactions were significant. Starting from these results we decided to use the four factor combinations of approach and responsiveness as a way to characterize the induction of animacy by interactive movement patterns between the two spheres (see Table 1 for mean animacy ratings for each category and additional descriptive statistics), and as a base for the parametric analysis of the fMRI data (see Statistical analyses of fMRI data). Pair-wise comparisons confirmed significant differences in subjective animacy ratings between all pairs of the selected stimulus categories (see Table 1) and thus demonstrate a significant discriminatory power and justify our stimulus category coding. Furthermore, subjective ratings of the four movement patterns showed a significant linear trend ($F(1) = 6.327$, $p < 0.001$), therefore supporting the ranking and the equidistance of the stimulus categories.

Table 1
Descriptive and inferential statistics for the four stimulus categories based on movement patterns. M = Mean, SD = Standard Deviation, CI = Confidence Interval. * p-Values that survived the Bonferroni-correction for multiple comparisons ($p < 0.008$).

			95% CI	
Movement patterns	*M*	SD	Lower bound	Upper bound
1. no approach + no responsiveness	2.036	0.419	1.794	2.278
2. no approach + responsiveness	2.641	0.546	2.326	2.956
3. approach + no responsiveness	3.055	0.384	2.833	3.276
4. approach + responsiveness	3.437	0.439	3.183	3.691
Pair-wise comparisons	*T*	*df*	*p*	*r*
1 vs. 2	−3.985	13	0.002*	0.74
2 vs. 3	−3.172	13	0.007*	0.66
3 vs. 4	−2.817	13	0.015	0.62
1 vs. 3	−12.214	13	0.000*	0.96
2 vs. 4	−8.260	13	0.000*	0.92
1 vs. 4	−9.690	13	0.000*	0.94

Neural correlates of animacy experience

Our primary focus was the identification of brain regions featuring an increase of neural activity associated with a linear increase or decrease in animacy experience, respectively (as a function of subjective ratings). We found that an increase in animacy experience was associated with higher activations in i) the bilateral insula (right insula: $T = 5.49$, $p < 0.001$; left insula: $T = 5.34$, $p < 0.001$), extending bilaterally to the superior temporal gyrus and sulcus, ii) the medial orbitofrontal cortex (mOFC) ($T = 4.89$, $p = 0.002$), extending to the pre- and subcallosal ACC, and iii) the left parahippocampal gyrus ($T = 6.21$, $p = 0.011$) extending into the left fusiform gyrus (FFG) (see Fig. 1, Table 2).

A decrease in animacy experience was associated with increased activations in i) the right postcentral gyrus ($T = 4.94$, $p = 0.007$) extending to the precentral gyrus and the inferior parietal lobe, ii) the right inferior frontal gyrus ($T = 4.58$, $p = 0.028$), and iii) the right precuneus ($T = 4.33$, $p = 0.029$) (see Fig. 1, Table 2).

Neural correlates of movement patterns

An increase in interactive movements based on approach and responsiveness, showed stronger neural activity in i) the insula bilaterally (right insula: $T = 6.77$, $p < 0.001$; left insula: $T = 5.82$, $p < 0.001$), extending to the right amygdala, the bilateral STG, and the right temporal pole, ii) the ACC bilaterally (maxima on the left: $T = 5.89$, $p < 0.001$), iii) the bilateral FFG (right FFG: $T = 5{,}49$, $p < 0.001$; left FFG: $T = 6.22$, $p < 0.001$), iv) the bilateral parahippocampal gyrus (maxima on the left: $T = 5.48$, $p < 0.001$), v) the left middle cingulate cortex ($T = 5.87$, $p = 0.001$), vi) the right paracentral lobule ($T = 6.01$, $p = 0.015$), and vii) the bilateral rolandic operculum (right operculum: $T = 6.98$, $p = 0.019$; left operculum: $T = 5.29$, $p = 0.031$) (see Fig. 2, Table 3).

A decrease in interactive movements based on movements of approach and responsiveness revealed increased neural activity in i) the precuneus ($T = 6.03$, $p < 0.001$), ii) the right middle frontal gyrus ($T = 4.66$, $p < 0.001$), extending to the inferior frontal gyrus, iii) the bilateral inferior parietal lobe (right IPL: $T = 4.72$, $p = 0.001$; left IPL: $T = 4.36$, $p = 0.012$), and iv) the left inferior frontal gyrus ($T = 5.21$, $p < 0.031$) (see Fig. 2, Table 3).

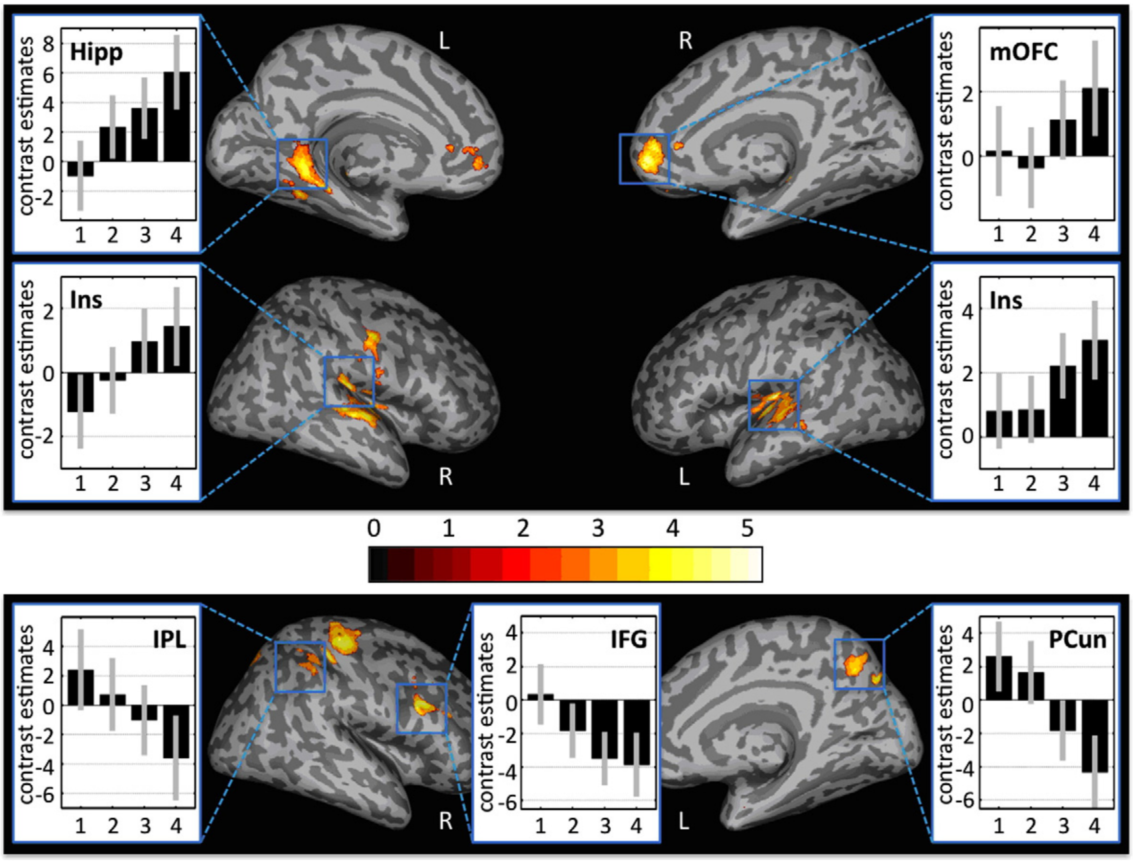

Fig. 1. Brain regions of increased activation for parametric modulation of animacy experience. Parametric modulation analysis of fMRI data identified the bilateral insula extending into the STS, the mOFC, and left parahippocampal gyrus extending into the FFG, where BOLD signal changes increased linearly with *increasing animacy experience* (upper box). Plots illustrate corresponding contrast estimates obtained for movies with different ratings for four different local maxima (upper left plot: Parahipp, $x = -14$, $y = -36$, $z = -13$; lower left plot: right Ins, $x = 38$, $y = -30$, $z = 23$; upper right plot: mOFC, $x = 12$, $y = 52$, $z = -1$; lower right plot: left Ins, $x = -32$, $y = -22$, $z = 19$). The same analysis revealed regions in right inferior frontal (IFG) and parietal lobules (IPL) as well as in the precuneus where BOLD signal changes increased linearly with *decreasing animacy experience* (lower box). Plots illustrate corresponding contrast estimates obtained for movies with different ratings for three different local maxima (left plot: IPL, $x = 54$, $y = -40$, $z = 53$; middle plot: IFG, $x = 44$, $y = 14$, $z = 31$; right plot: PCun, $x = 16$, $y = -70$, $z = 43$). The SPM{t} maps of these contrasts were overlaid on lateral and medial views of a surface based representation of the MNI canonical brain. The bar represents the color coding of the t-values for overlaid SPM{t} maps; mOFC = medial orbitofrontal cortex; Hipp = parahippocampal gyrus; Ins = Insula; IPL = inferior parietal lobule; PCun = Precuneus; IFG = inferior frontal gyrus.

Discussion

The present study focused on activation patterns of the brain related to the subjective experience of animacy in a parametric design, and on the influence of specific movement parameters contributing to the subjective experience. Results show that with increasing animacy experience, key regions part of the Social Neural Network (SNN) were recruited, while decreasing experience of animacy was associated with activation of fronto-parietal regions previously associated with the human Mirror Neuron System (hMNS). We argue that the hMNS may constitute a neural module for the "detection" and "interpretation" of actions, expressed in movement variations in general. Conversely, when stimuli appear highly animated, as in the case of movements invoking social intentions (such as "approach"), the SNN is recruited, assumed to be responsible for the adequate interpretation or the "evaluation" of relevant social cues.

Increasing animacy experience

Regions of increased neural activity that correlate with increasing experience of animacy, namely the insula, the mOFC and the ACC, the STG/STS and the FFG, are key regions in social neuroscience.

The strongest increase in activity bilaterally was shown in the insula, extending to the posterior STG/STS. The role of the insula, as part of the SNN (Adolphs, 1999; Blakemore, 2008; Frith and Frith, 2006), has recently become more prominent due to its involvement in decision-making processes (Huettel, 2006; Kuhnen and Knutson, 2005; Paulus et al., 2003; Preuschoff et al., 2008), as well as in the perception of fear (Phillips et al., 1997) and disgust (Anderson et al., 2003; Phillips et al., 2004; Phillips et al., 1997), and empathy for others (Jabbi et al., 2007; Saarela et al., 2007; Singer et al., 2004). Only very recently, models on the functional role of the insular cortex have been proposed. One of these models links the insula to a functional role in awareness (Craig, 2009), as a site where inputs from interoceptive signals are integrated with signals of emotionally salient stimuli coming from the TP and the amygdala. Subjective awareness is processed in the insula by integrating motivational, social and cognitive conditions represented in other parts of the brain such as the mPFC. Another recent model on the function of the insula implicates this region in affective learning that could guide decision making in uncertain environments (Singer et al., 2009). This model is supported by research in decision making that show a strong link between insular activation, particularly the anterior insula, and processing, representing and learning information about risk and uncertainty (Huettel, 2006; Paulus et al., 2003; Preuschoff et al., 2008). Increasing animacy experience revealed an increased

Table 2
Neural correlates of animacy experience. Results of the random-effects analysis with linear parametric modulation of the BOLD-response to stimulus movies by subjects' ratings. Included are: (i) the contrast identifying regions with increased neural activation corresponding to increasing animacy experience; and (ii) the contrast identifying neural regions with increased neural activation corresponding to decreasing animacy experience. For each presented cluster, coordinates at the maximum voxel are reported in the same row as the cluster size. Within extended clusters, coordinates for additional local maxima are indicated in rows below the respective cluster size declaration. Distinct clusters are separated with white lines. *x*, *y* and *z* refer to the MNI stereotactic coordinates. R = right hemisphere; L = left hemisphere; STG = superior temporal gyrus; STS = superior temporal sulcus; mOFC = medial orbitofrontal cortex; ACC = anterior cingulate cortex; FFG = fusiform gyrus.

Region	Cluster size	Cluster p_c	Side	x	y	z	T
Increasing animacy experience							
Insula	1160	0.000	R	38	−30	23	5.49
STG			R	46	−20	3	5.02
Postcentral gyrus			R	50	−8	35	4.17
Insula	885	0.000	L	−32	−22	19	5.34
STG			L	−44	−16	1	5.08
STS			L	−60	−20	1	4.27
mOFC	518	0.002	R	12	52	−1	4.89
ACC			R	2	40	−3	4.29
Parahippocampal gyrus	409	0.011	L	−14	−36	−13	6.21
Lingual gyrus			L	−14	−42	−3	4.37
FFG			L	−28	−50	−11	4.08
Decreasing animacy experience							
Postcentral gyrus	439	0.007	R	40	−32	55	4.94
Precentral gyrus			R	40	−26	61	4.03
Inferior parietal lobule			R	54	−40	53	3.08
Inferior frontal gyrus	339	0.028	R	44	14	31	4.58
			R	58	14	31	3.56
Precuneus	337	0.029	R	16	−70	43	4.33

activity in posterior insular cortex, replicating previous findings in animacy research (Gobbini et al., 2007; Wheatley et al., 2007), while increasing complexity of interactive movements extended this activation to the medial and anterior insula. Based on the above mentioned functional models on the insula, we suggest that meaningful social cues, such as movements of approach and responsiveness, represent salient information that – through the set of movies – helped the subjects to base their decisions on what they felt as more animated or less so. Because they had to use a scale to make their judgements (instead of using a binary system) the more anterior sites of the insula come into play associated with an affective learning component, by integrating stimuli-related emotionally relevant information signalled from the TP and the amygdala (areas that were activate during increasing interactive movements, but not during increasing animacy experience). The movement cues in our movies have an ambiguous nature in the sense that subtle changes in movement patterns could lead to animacy experiences that differed from subject to subject (subjective animacy experience). Due to the ambiguous cues used in our movies, we suggest that affective learning in the insula helped guiding the animacy judgements, which – together with the integration of emotional, social and cognitive information – led to an animacy-related subjective experience processed in more posterior areas of the insula. Our hypothesis is in line with the recent model on the insula proposed by Singer et al. (2009) emphasizing its role in affective learning, as well as in the integration of social information with information coming from external uncertain/ambiguous cues.

On the basis of the literature it is plausible to speculate that the integration of information in the insula is further processed by strongly connected cortical areas responsible for the evaluation of the potentially socially enriched material, including the mOFC and the ACC in the vmPFC, which were among the strongest activated regions associated with increasing animacy experience. This region has been previously linked to mentalizing capacities or person perception (Amodio and Frith, 2006), and the observation of communicative intentions (Amodio and Frith, 2006; Becchio et al., 2006; Grezes et al., 2004; Walter et al., 2004). Thus, studies point to a functional dissociation within frontal dorsal/medial areas. Activity in the ventral mPFC is involved in social and emotional processes (Bush et al., 2000; Whalen et al., 1998), whereas the dorsal mPFC is involved in more cognitive processes such as resolving cognitive conflicts (present in tasks such as the Stroop task) (Botvinick et al., 2004; Carter et al., 1998). Specifically, the ventral mPFC seems to play a role in social and emotional evaluation (Somerville et al., 2006). In conformity, our results point to a role of the ventral mPFC in the evaluation of animated movements and processing social cues. Walter et al. (2004) in particular, proposed that the ventral mPFC is mainly involved in mentalizing processes that are embedded in a context of social interaction, while private intentions are processed in a more dorsal region (Walter et al., 2004). Our present findings are in accordance with this hypothesis. The animations always showed two spheres in which increasing animacy experience and interactive movements (approach and responsiveness) resulted in increased ventral mPFC activation. Moreover, the same region has previously been shown to be activated by the perception of socially relevant facial expressions and by being personally addressed in a (virtual) social interaction (Schilbach et al., 2006), and during the experience of an “online” interaction with a virtual other in a gaze-contingency paradigm (Schilbach et al., 2009). Socially relevant facial expressions might feed the same evaluation process that is also involved during the judgment of animated scenes as presented in the current experiment, irrespective of whether the stimuli are human-looking or context-embedded (Wheatley et al., 2007). Closely related to our findings are the results from a study using computer-animated characters to investigate biological motion perception (Chaminade et al., 2007) that found the vmPFC to be positively correlated with the tendency to perceive motion as natural. Our study hence provides further evidence that the vmPFC sustains the subjective perception of the stimuli rather than their physical features such as anthropomorphic properties.

Importantly, our instructions were not meant to elicit mentalizing attributions, as we wanted to keep the subjects as free as possible when generating their individual judgments related to their own interpretation of the movements. Therefore, our instructions did not provide any indication as to the animacy degree content in our stimuli. Previous studies using geometric shapes did not find any differences in the amount of mental state inferences when comparing explicit and non-cued instructions (Castelli et al., 2000). In the same line, despite the lack of explicit instructions regarding mental state ascription (“What was happening in this animation?”) Castelli et al. (2002) still could demonstrate spontaneous mentalizing contents in neurotypical participants' responses, as well as activations in the ToM network. Furthermore, the events in our animations are very simple, the most common and “typical” verbal description of the participating subjects obtained after the experiment that can be related to mentalizing (associated with the highest rated movies) was: “the sphere seemed to know the other sphere” (that is why it stopped) “and approached to talk”. In conclusion, we argue that animations including socially meaningful movement patterns automatically elicit spontaneous mentalizing processes that lead to the attribution of personality or animacy. Consequently, the supposed spontaneous mentalizing in the context of animacy perception could explain the involvement of the vmPFC as a part of the ToM network.

We also found activation of the fusiform gyrus (FFG), which has been introduced as the “face recognition” area (Kanwisher et al., 1997). This view, however, has recently been challenged by the “expertise hypothesis” proposing that the FFG is recruited during categorizing tasks in which participants have reached a significant expertise, whether these are faces or object categories (Bukach et al., 2006;

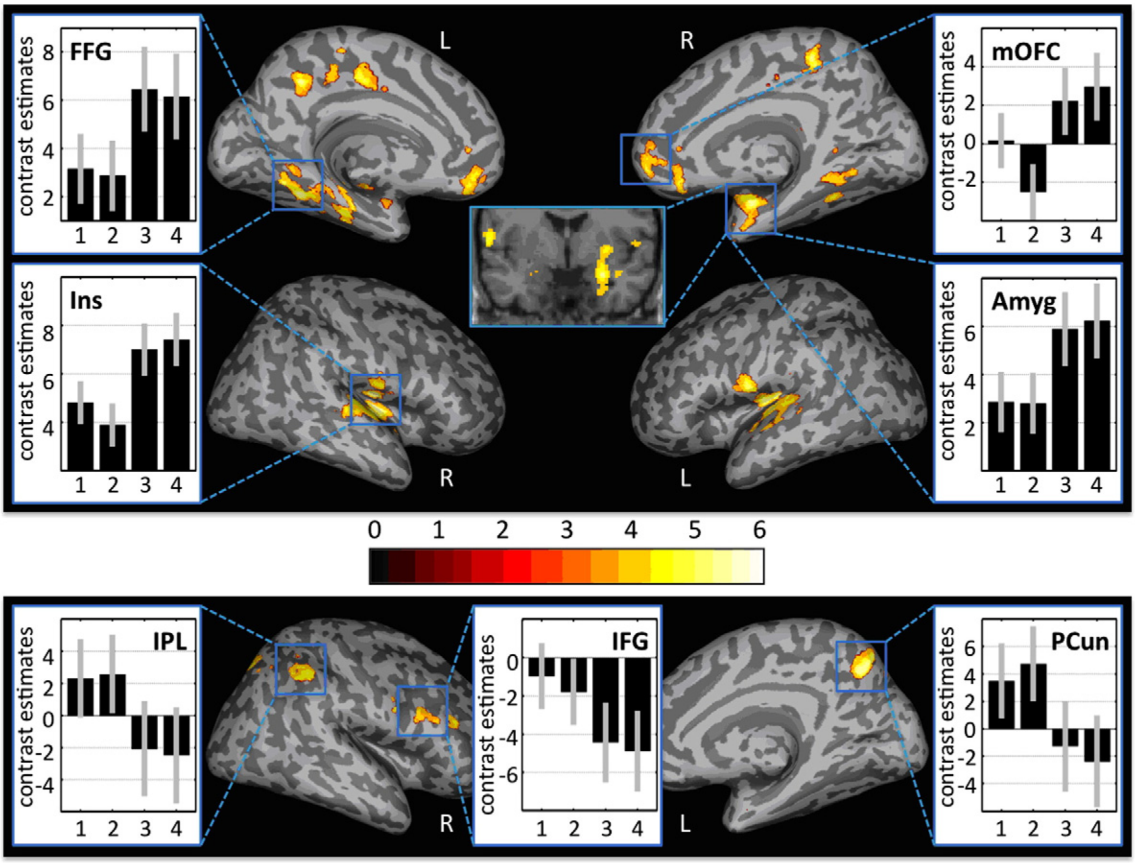

Fig. 2. Brain regions of increased activation for parametric modulation of interactive movements between the spheres (approach and responsiveness). Parametric modulation analysis of fMRI data identified regions in bilateral insula extending into the STG, right amygdala and temporal pole, mOFC and bilateral parahippocampal gyrus, FFG and middle cingulate gyrus where BOLD signal changes increased linearly with *increasing interactive movements* (upper box). Plots illustrate corresponding contrast estimates obtained for movies with different movement patterns (1 = no interactive movement between the spheres to 4 = both movements of approach and responsiveness) for four different local maxima (upper left plot: FFG, $x = -28$, $y = -50$, $z = -11$; lower left plot: right Ins, $x = 36$, $y = -12$, $z = 5$; upper right plot: mOFC, $x = 10$, $y = 54$, $z = -5$; lower right plot: right Amyg, $x = 28$, $y = -2$, $z = -19$). The same analysis revealed regions in bilateral inferior frontal and parietal lobules as well as in the precuneus where BOLD signal changes increased linearly with *decreasing interactive movements* (lower box). Plots illustrate corresponding contrast estimates obtained for movies with different movement patterns (see above) for three different local maxima (left plot: IPL, $x = 54$, $y = -44$, $z = 51$; middle plot: IFG, $x = 58$, $y = 10$, $z = 23$; right plot: PCun, $x = 6$, $y = -68$, $z = 45$). The SPM{t} maps of these contrasts were overlaid on lateral and medial views of a surface based representation of the MNI canonical brain; mOFC = medial orbitofrontal cortex; Amyg = Amygdala; FFG = fusiform gyrus; Ins = Insula; IPL = inferior parietal lobule; PCun = Precuneus; IFG = inferior frontal gyrus. Statistical threshold: $p < 0.0005$ at the voxel level, uncorrected and $p < 0.05$ at the cluster-level, corrected.

Gauthier et al., 2000; Gauthier et al., 1999; Golby et al., 2001). Supporting the expertise hypothesis, animacy studies addressing mentalizing processes frequently reported FFG activations in the absence of facial features in the stimuli (Castelli et al., 2002; Castelli et al., 2000; Gobbini et al., 2007; Martin and Weisberg, 2003; Schultz et al., 2005; Tavares et al., 2008; Wheatley et al., 2007). We suggest that the FFG activation evoked by increased animacy experience and movements of approach might be related to the high expertise of humans for socially appearing animated movements, since humans are highly specialized in and attuned to social relevant signs (Tomasello et al., 2005).

Increased STS/STG bilateral activation associated with increased animacy experience and with increase in interactive movements, is congruent with previous reports implicating the STS/STG in the perception of biological motion (Beauchamp et al., 2002, 2003; Bonda et al., 1996; Grezes and Decety, 2002; Grezes et al., 2001; Grossman et al., 2000; Grossman and Blake, 2001; Howard et al., 1996; Pelphrey et al., 2003; Vaina et al., 2001), in processing the kinematics of geometrical figures (Blakemore et al., 2003; Schultz et al., 2005, 2004), and in processing realistic scenes (Mar et al., 2007). More specifically, it has been proposed that the STS may be important for the processing of intentional action (Blakemore et al., 2003; Saxe et al., 2004; Schultz et al., 2004). The lateralization of such responses, however, is still a matter of conjecture. Ciaramidaro et al. (2007) proposed that the left STS is mainly related to the processing of communicative intention, while the right STS may play a role in understanding others intentions (Ciaramidaro et al., 2007). Recently, de Lange et al. (2008) also found the right STS to specifically activate when participants in their study selectively attended to the intentionality of an action (de Lange et al., 2008). Saxe et al. (2004) showed their participants videos of an actor walking and stopping for a certain period of time behind a bookcase (Saxe et al., 2004). They found activation in the right STS related to longer occlusions, suggesting that this region is involved in the representation of observed intentional actions. Contradicting previous behavioural results (Santos et al., 2008), we were surprised to verify that in the present study using the same paradigm, time delay did not constitute a significant cue for animacy experience, neither at the behavioural level (please see section Results for the behavioural data), nor at the neural level (even when using a lower threshold). One possible explanation for the difference between the results in the present study and the results observed in the Saxe et al. (2004) paradigm lies on the fundamental difference between the types of characters involved. Wherefore, watching a human hide behind a box may lead to stronger effects related to mental attributions (such as intentional inferences) than watching a sphere stopping for varied amounts of time.

Table 3
Neural correlates of movement patterns. Results of the random-effects analyses with linear parametric modulation of the BOLD-response to stimulus movies by interactive movement patterns between the spheres. Included are: (i) the contrast identifying regions with increased neural activation corresponding to increases in interactive movements; (ii) the contrast identifying neural regions with increased neural activation corresponding to decreases in interactive movements. For each presented cluster, coordinates at the maximum voxel are reported in the same row as the cluster size. Within extended clusters, coordinates for additional local maxima are indicated in rows below the respective cluster size declaration. Distinct clusters are separated with white lines. *x*, *y* and *z* refer to the MNI stereotactic coordinates. R = right hemisphere, L = left hemisphere. STG = superior temporal gyrus; STS = superior temporal sulcus; ACC = anterior cingulate cortex; mOFC = medial orbitofrontal cortex; FFG = fusiform gyrus.

Region	Cluster size	Cluster p_c	Side	x	y	z	T
Increasing interactive movement approach + responsiveness							
Insula	1303	0.000	R	36	−12	5	6.77
Amygdala			R	28	−2	−19	6.00
STG			R	54	−22	9	4.91
Rolandic operculum			R	60	−4	17	4.88
Temporal pole			R	40	4	−23	4.16
Parahippocampal gyrus			R	34	−10	−25	3.95
Insula	843	0.000	L	−36	−16	17	5.82
STG			L	−44	−18	5	5.39
STS			L	−54	−18	−5	4.38
ACC	640	0.000	L	−2	46	−7	5.89
mOFC			R	10	54	−5	4.83
Rectal gyrus			L	−4	42	−15	5.13
			R	6	30	−19	4.86
FFG	331	0.000	L	−28	−50	−11	6.22
Lingual gyrus			L	−26	−56	−7	5.30
Parahippocampal gyrus			L	−22	−30	−15	3.97
Parahippocampal gyrus	318	0.000	L	−20	−14	−19	5.48
FFG			L	−34	−28	−15	4.05
FFG	290	0.000	R	22	−46	−11	5.49
Lingual gyrus			R	16	−58	−11	5.42
Parahippocampal gyrus			R	26	−44	−3	4.16
Middle cingulate cortex	212	0.001	L	−12	−46	37	5.87
Paracentral lobule	121	0.015	R	14	−38	49	6.01
Rolandic operculum	114	0.019	R	46	−8	19	6.98
Middle cingulate cortex	113	0.020	L	−6	−14	43	5.17
Rolandic operculum	101	0.031	L	−58	−2	9	5.29
Decreasing interactive movement approach + responsiveness							
Precuneus	524	0.000	R	6	−68	45	6.03
Middle frontal gyrus	297	0.000	R	46	32	23	4.66
Inferior frontal gyrus			R	58	10	23	4.65
Inferior parietal lobule	207	0.001	R	54	−44	51	4.72
Inferior parietal lobule	128	0.012	L	−36	−38	45	4.36
Angular gyrus			L	−30	−52	37	3.97
Inferior frontal gyrus	101	0.031	L	−42	26	27	5.21

Increase in interactive movements (approach and responsiveness)

Corroborating the subjective experience of increased animacy a very similar pattern was found associated with increasing complexity of social cues, expressed as an increase in interactive movements between the spheres, namely in a wide range of brain areas implicated as part of the SNN, including the insula, activation extending to the STG, the amygdala, the parahippocampal gyrus and the temporal pole (TP), the mOFC, the FFG, and others.

We have already discussed before the specific role of the insula. With increasing complexity of interactive movements between the spheres (movements of approach and responsiveness) the increased activation in the posterior insula extended forward to the medial and anterior insula, the amygdala and the TP.

The TP, as part of the SNN (Amodio and Frith, 2006; Blakemore, 2008; Frith, 2007; Pinkham et al., 2003) was recently discussed to process complex social stimuli based on narrative or scripts (Castelli et al., 2000; Olson et al., 2007), abstract conceptual knowledge of social behaviours (Zahn et al., 2007), and is found in "classical" ToM studies (Fletcher et al., 1995; Vogeley et al., 2001). Here we show that the TP is also responsive to comparably simple animated movement that introduces social narrative into the display. The parahippocampal gyrus, functionally close related to the TP, and the hippocampus were also found to be activate. Previous studies point to a role of the parahippocampal regions in contextual (Rauchs et al., 2008) and autobiographical memory (Fink et al., 1996; Maguire, 2001; Maguire et al., 2000). Maguire et al. (2000) observed increased connectivity between the parahippocampal gyrus and the temporal pole associated with retrieval of autobiographical events. Activations in these areas may hence reflect the access to social semantic information while decoding the displayed movements.

With strong connections to the insula (Hoistad and Barbas, 2008), the TP and the OFC (Adolphs, 2003; Davidson and Irwin, 1999), the amygdala, as part of the SNN (Adolphs, 1999, 2001, 2003; Blakemore, 2008; Brothers, 1990; Frith, 2007; Pinkham et al., 2008; Skuse and Gallagher, 2009), have been associated to the evaluation of emotional significance in social contexts (Adolphs, 2003). Its role in associating valence to stimuli (Kim et al., 2003; Pessoa et al., 2005; Straube et al., 2008) and its activation by stimulus intensity, but not value (Anderson and Sobel, 2003; Small et al., 2003), has led to a recent hypothesis that the amygdala actually codes an interaction between intensity and valence of the stimuli, reflecting the overall emotional value of a stimulus (Dolan, 2007). In accordance, it also modulates emotional behaviour during biologically-relevant situations (Herry et al., 2007). Moreover, it has been suggested that the amygdala is involved in vigilance for salient stimuli that are unpredictable or ambiguous (Adolphs, 2009; Whalen, 2007). The involvement of the amygdala for increases in interactive movements might have been necessary to evaluate the salience in movement changes, as part of socially meaningful contexts. Thus, it is quite plausible, considering the activation of the amygdala for increases in interactive movements but not for increases in animacy experience that the amygdala played an important role in the evaluation of social physical cues present in the stimuli by coding for its overall emotional/social value.

The large activation of the mOFC (as part of the vmPFC), and the overlap with the effects of increases in animacy experience reiterates the important contribution of interactive elements in the perception of animacy and the role of the vmPFC in perceiving them.

Decreasing animacy experience

A decrease in animacy experience activated the inferior parietal lobe (IPL) bilaterally and the right inferior frontal gyrus (IFG), which have previously been described as part of the hMNS (Hamilton and Grafton, 2007; Rizzolatti and Craighero, 2004), the postcentral gyrus and the precuneus.

The precuneus has been previously implicated in visuo-spatial imagery, in shifting attention between targets, and in encoding as well as retrieval of spatial locations (Burgess and Shallice, 1996; Cavanna and Trimble, 2006; Frings et al., 2006; Misaki et al., 2002; Rao et al., 2003; Wheatley et al., 2007). Thus, the parietal cortex together with the precuneus, cooperates in directing attention in space during mentally tracking targets (Culham et al., 1998). Increases in precuneus activation have also been reported during processing of animated stimuli (Ochsner et al., 2004; Wheatley et al., 2007), real stimuli when compared to animated (Mar et al., 2007) and perspective taking (Chaminade and Decety, 2002; Farrer and Frith, 2002; Ruby and Decety, 2001; Vogeley et al., 2004), suggesting that this region serves the function of a spatial workspace within the ToM network. Its increased activity during decreased animacy experience, suggests that the involvement of the precuneus links to the processing of dynamic scenes, more related to spatial dynamics than to social animacy inference. The relevance of such a visuo-spatial workspace in social cognition is evident, since dynamic scenes have to be evaluated for their spatial and temporal contingency in order to allow recognition of social cues.

Activity in the precuneus has also been shown in self-processing experiments. Vogeley et al. (2001) found precuneus activations for first person perspective during mental attributions to oneself. Similarly, precuneus activations were found in studies involving self-reflection (Johnson et al., 2002; Lou et al., 2004). Den Ouden et al. (2005) found convergent precuneus activation both for intentional causality and prospective memory, leading to the suggestion of the precuneus specific involvement in processing intentions related to the self (den Ouden et al., 2005). Together with the recent implication of the precuneus as part of the brain default mode (Gusnard and Raichle, 2001) – corresponding to a metabolic resting state – a decrease in animacy experience might reflect a state of relaxation allowing a reorientation to the subject's own thoughts, when demands to focus on social signals embedded in the animated stimuli decrease.

The hMNS concept is an extension of the earlier description of mirror neurons activated by execution and observation of actions in monkeys (Gallese et al., 1996; Rizzolatti et al., 2001). The putative localization for the hMNS includes the left and right IPL and the right IFG (Hamilton and Grafton, 2007; Rizzolatti and Craighero, 2004). Research has shown these brain areas to be implicated in action perception, whether the actions are performed (Grafton et al., 1992), imagined (Grafton et al., 1996; Iacoboni et al., 1999), observed (Buccino et al., 2001, 2004), or imitated (Aziz-Zadeh et al., 2006; Buccino et al., 2004; Iacoboni et al., 1999). The "motor resonance function" of the hMNS has been related to empathy (Iacoboni and Dapretto, 2006). Furthermore, the hMNS seems to play a role in differentiating intentional actions that are part of everyday life (for example, grasping to drink) (Iacoboni et al., 2005). Particularly, the lateral parietal lobe responds to changes in movement direction (Donner et al., 2007; Martinez-Trujillo et al., 2007; Shulman et al., 2001) and is associated with spatial attention (Corbetta and Shulman, 2002) while the inferior frontal gyrus is involved in task switching (Brass et al., 2007), which suggests that these regions contribute to action understanding.

In the present study only the SNN but not the hMNS was modulated by increasing animacy experience. In accordance, Wheatley et al. (2007) investigated brain activity evoked by interpreting and imagining moving shapes as animate or inanimate. They found the hMNS to be active during both motion observation and imagery but not modulated by animacy. Similarly, perceiving motion as natural/biological positively correlated with the SNN, but negatively correlated with the hMNS (Chaminade et al., 2007). Thus, recent studies found the hMNS to respond to both human and robotic actions (Gazzola et al., 2007), as well as to movements not belonging to the human motor repertoire (Engel et al., 2008). As increased activation of the hMNS was also found during the decrease in interactive movements in the movies, it appears that the hMNS 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. In particular, we would like to argue that the hMNS is not specifically involved in animacy perception or detection of social cues, or, at least, it is involved to a lower degree once socially significant signals become relevant. Along the same line, we hypothesize that paradigms that concern making decisions as to observed intentions and social inferences might require brain areas that integrate a wide range of social information and decision-making processing. Therefore, once decisions about social content have to be made, and the degree of social computation increases, the SNN is recruited to take over. The hMNS function in social perception and in action perception appears to be necessary to process intentionality and imitation, but not necessarily social and not necessarily animated or biological, in the sense of relevant action "detection" whereas the action "evaluation" is a key property of the SNN.

On a more speculative note, we would like to propose that while increasing animacy experience recruits sites involved with higher cognition that are required for computation and interpretation of social movements (including brain regions involved in access to semantic social memories) – correspondent to a more cognitive-controlled system of processing – a decrease in animacy experience would rather involve more low-level processing of features, an early evolutionary system involving sites of automatic movement perception processing. While decreasing animacy experience would rely on a neural system evolutionarily shared with other animals – the MNS – the increasing animacy experience would rely on a neural system strongly dependent on anterior–frontal structures such as the prefrontal cortex, which would constitute our "social cognition" site of evolutionary complexity gain — the SNN. As such, humans are capable of disentangling and interpreting very subtle social cues in other movements, to make decisions concerning social content, and then also able to trigger a quite advanced system of interpretation capacity such as mentalizing.

Conclusions

The present research used a parametric approach to explore brain activations during increases and decreases in animacy experience and to understand how certain movement parameters contribute to this experience. Firstly, our study corroborates that also simple geometric figures can convey the impression of social encounters if they express a certain pattern of movements that allow ascribing animacy to these figures. Secondly, a subjective increase in animacy experience relates to increased activation in key brain areas of the SNN, dedicated to the subjective experience of being in the presence of entities that are perceived as social agents and necessary for the computation of social cues. We also showed that interactive movements, such as movements of approach, constitute a prime animacy property for social content perception. Thirdly, decreasing animacy experience, and decreases in interactive movements correlated with increased activations of the hMNS, suggesting that the hMNS is involved in pre-inferential processes that appear as necessary but most likely not as a sufficient precondition for animacy perception or for decision-making processes concerning social inferences. Finally, the implications of the present study foster future neuroimaging research to apply parametric methods to access differential components in the study of animacy perception and in clinical studies related to neuropsychiatric disorders such as autism and schizophrenia that typically show difficulties of social nature.

Acknowledgments

We would like to thank Barbara Elghahwagi and Cordula Kemper for their assistance with the fMRI scanning; Carolin Aumann for help with the subject's recruitment; and Bettina Bewernick, Alexandra Georgescu, Astrid Gawronski, Hanna Kockler, Leonhard Schilbach, and Ralf Tepest for their valuable comments on the study. This work was supported by the German Volkswagen-Stiftung (Kai Vogeley) and the Portuguese scientific foundation Fundação para a Ciência e Tecnologia (FCT), the latest in the form of a fellowship to Natacha Santos.

References

Abell, F., Happe, F., Frith, U., 2000. Do triangles play tricks? Attribution of mental states to animated shapes in normal and abnormal development. Cognitive Dev. 15, 1–16.
Adolphs, R., 1999. Social cognition and the human brain. Trends Cogn. Sci. 3 (12), 469–479.
Adolphs, R., 2001. The neurobiology of social cognition. Curr. Opin. Neurobiol. 11 (2), 231–239.
Adolphs, R., 2003. Cognitive neuroscience of human social behaviour. Nat. Rev. Neurosci. 4 (3), 165–178.
Adolphs, R., 2009. The social brain: neural basis of social knowledge. Annu. Rev. Psychol. 60, 693–716.
Amodio, D.M., Frith, C.D., 2006. Meeting of minds: the medial frontal cortex and social cognition. Nat. Rev. Neurosci. 7 (4), 268–277.

Anderson, A.K., Sobel, N., 2003. Dissociating intensity from valence as sensory inputs to emotion. Neuron 39 (4), 581–583.

Anderson, A.K., Christoff, K., Panitz, D., De Rosa, E., Gabrieli, J.D., 2003. Neural correlates of the automatic processing of threat facial signals. J. Neurosci. 23 (13), 5627–5633.

Aziz-Zadeh, L., Koski, L., Zaidel, E., Mazziotta, J., Iacoboni, M., 2006. Lateralization of the human mirror neuron system. J. Neurosci. 26 (11), 2964–2970.

Barrett, H., Todd, P., Miller, F., Blythe, M., 2005. Accurate judgments of intention from motion cues alone: a cross-cultural study. Evol. Hum. Behav. 26, 313–331.

Bassili, J.N., 1976. Temporal and spatial contingencies in the perception of social events. J. Pers. Soc. Psychol. 33 (6), 680–685.

Beauchamp, M.S., Lee, K.E., Haxby, J.V., Martin, A., 2002. Parallel visual motion processing streams for manipulable objects and human movements. Neuron 34 (1), 149–159.

Beauchamp, M.S., Lee, K.E., Haxby, J.V., Martin, A., 2003. FMRI responses to video and point-light displays of moving humans and manipulable objects. J. Cogn. Neurosci. 15 (7), 991–1001.

Becchio, C., Adenzato, M., Bara, B.G., 2006. How the brain understands intention: different neural circuits identify the componential features of motor and prior intentions. Conscious. Cogn. 15 (1), 64–74.

Beer, J.S., Ochsner, K.N., 2006. Social cognition: a multi level analysis. Brain Res. 1079 (1), 98–105.

Bifulco, A., Kwon, J., Jacobs, C., Moran, P.M., Bunn, A., Beer, N., 2006. Adult attachment style as mediator between childhood neglect/abuse and adult depression and anxiety. Soc. Psychiatry Psychiatr. Epidemiol. 41 (10), 796–805.

Blake, R., Shiffrar, M., 2007. Perception of human motion. Annu. Rev. Psychol. 58, 47–73.

Blakemore, S.J., 2008. The social brain in adolescence. Nat. Rev. Neurosci. 9 (4), 267–277.

Blakemore, S.J., Fonlupt, P., Pachot-Clouard, M., Darmon, C., Boyer, P., Meltzoff, A.N., et al., 2001. How the brain perceives causality: an event-related fMRI study. NeuroReport 12 (17), 3741–3746.

Blakemore, S.J., Boyer, P., Pachot-Clouard, M., Meltzoff, A., Segebarth, C., Decety, J., 2003. The detection of contingency and animacy from simple animations in the human brain. Cereb. Cortex 13 (8), 837–844.

Bonda, E., Petrides, M., Ostry, D., Evans, A., 1996. Specific involvement of human parietal systems and the amygdala in the perception of biological motion. J. Neurosci. 16 (11), 3737–3744.

Botvinick, M.M., Cohen, J.D., Carter, C.S., 2004. Conflict monitoring and anterior cingulate cortex: an update. Trends Cogn. Sci. 8 (12), 539–546.

Brass, M., Schmitt, R.M., Spengler, S., Gergely, G., 2007. Investigating action understanding: inferential processes versus action simulation. Current Biology 17 (24), 2117–2121.

Brothers, L., 1990. The social brain: a project for integrating primate behaviour and neurophysiology in a new domain. Concepts Neurosci. vol. I, 27–51.

Buccino, G., Binkofski, F., Fink, G.R., Fadiga, L., Fogassi, L., Gallese, V., et al., 2001. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. Eur. J. Neurosci. 13 (2), 400–404.

Buccino, G., Vogt, S., Ritzl, A., Fink, G.R., Zilles, K., Freund, H.J., et al., 2004. Neural circuits underlying imitation learning of hand actions: an event-related fMRI study. Neuron 42 (2), 323–334.

Bukach, C.M., Gauthier, I., Tarr, M.J., 2006. Beyond faces and modularity: the power of an expertise framework. Trends Cogn. Sci. 10 (4), 159–166.

Burgess, P.W., Shallice, T., 1996. Confabulation and the control of recollection. Memory 4 (4), 359–411.

Bush, G., Luu, P., Posner, M.I., 2000. Cognitive and emotional influences in anterior cingulate cortex. Trends Cogn. Sci. 4 (6), 215–222.

Campbell, R., Lawrence, K., Mandy, W., Mitra, C., Jeyakuma, L., Skuse, D., 2006. Meanings in motion and faces: developmental associations between the processing of intention from geometrical animations and gaze detection accuracy. Dev. Psychopathol. 18 (1), 99–118.

Carter, C.S., Braver, T.S., Barch, D.M., Botvinick, M.M., Noll, D., Cohen, J.D., 1998. Anterior cingulate cortex, error detection, and the online monitoring of performance. Science 280 (5364), 747–749.

Castelli, F., Happe, F., Frith, U., Frith, C., 2000. Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. Neuroimage 12 (3), 314–325.

Castelli, F., Frith, C., Happe, F., Frith, U., 2002. Autism, Asperger syndrome and brain mechanisms for the attribution of mental states to animated shapes. Brain 125 (Pt 8), 1839–1849.

Cavanna, A.E., Trimble, M.R., 2006. The precuneus: a review of its functional anatomy and behavioural correlates. Brain 129 (Pt 3), 564–583.

Chaminade, T., Decety, J., 2002. Leader or follower? Involvement of the inferior parietal lobule in agency. NeuroReport 13 (15), 1975–1978.

Chaminade, T., Hodgins, J., Kawato, M., 2007. Anthropomorphism influences perception of computer-animated characters' actions. Soc. Cogn. Affect. Neurosci. 2, 206–216.

Ciaramidaro, A., Adenzato, M., Enrici, I., Erk, S., Pia, L., Bara, B.G., et al., 2007. The intentional network: how the brain reads varieties of intentions. Neuropsychologia 45 (13), 3105–3113.

Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev. Neurosci. 3 (3), 201–215.

Craig, A.D., 2009. How do you feel — now? The anterior insula and human awareness. Nat. Rev. Neurosci. 10 (1), 59–70.

Culham, J.C., Brandt, S.A., Cavanagh, P., Kanwisher, N.G., Dale, A.M., Tootell, R.B., 1998. Cortical fMRI activation produced by attentive tracking of moving targets. J. Neurophysiol. 80 (5), 2657–2670.

Davidson, R.J., Irwin, W., 1999. The functional neuroanatomy of emotion and affective style. Trends Cogn. Sci. 3 (1), 11–21.

de Lange, F.P., Spronk, M., Willems, R.M., Toni, I., Bekkering, H., 2008. Complementary systems for understanding action intentions. Curr. Biol. 18 (6), 454–457.

den Ouden, H.E., Frith, U., Frith, C., Blakemore, S.J., 2005. Thinking about intentions. Neuroimage 28 (4), 787–796.

Dittrich, W.H., Lea, S.E., 1994. Visual perception of intentional motion. Perception 23 (3), 253–268.

Dolan, R.J., 2007. The human amygdala and orbital prefrontal cortex in behavioural regulation. Philos. Trans. R. Soc. Lond. B Biol. Sci. 362 (1481), 787–799.

Donner, T.H., Siegel, M., Oostenveld, R., Fries, P., Bauer, M., Engel, A.K., 2007. Population activity in the human dorsal pathway predicts the accuracy of visual motion detection. J. Neurophysiol. 98 (1), 345–359.

Duvernoy, H.M., 1999. The Human Brain Surface, Three-Dimensional Sectional Anatomy with MRI, and Blood Supply. Springer, Vienna.

Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., et al., 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. Neuroimage 25 (4), 1325–1335.

Eickhoff, S.B., Paus, T., Caspers, S., Grosbras, M.H., Evans, A.C., Zilles, K., et al., 2007. Assignment of functional activations to probabilistic cytoarchitectonic areas revisited. Neuroimage 36 (3), 511–521.

Engel, A., Burke, M., Fiehler, K., Bien, S., Rosler, F., 2008. How moving objects become animated: the human mirror neuron system assimilates non-biological movement patterns. Soc. Neurosci. 3 (3–4), 368–387.

Farrer, C., Frith, C.D., 2002. Experiencing oneself vs another person as being the cause of an action: the neural correlates of the experience of agency. Neuroimage 15 (3), 596–603.

Fink, G.R., Markowitsch, H.J., Reinkemeier, M., Bruckbauer, T., Kessler, J., Heiss, W.D., 1996. Cerebral representation of one's own past: neural networks involved in autobiographical memory. J. Neurosci. 16 (13), 4275–4282.

Fletcher, P.C., Happe, F., Frith, U., Baker, S.C., Dolan, R.J., Frackowiak, R.S., et al., 1995. Other minds in the brain: a functional imaging study of “theory of mind” in story comprehension. Cognition 57 (2), 109–128.

Frings, L., Wagner, K., Quiske, A., Schwarzwald, R., Spreer, J., Halsband, U., et al., 2006. Precuneus is involved in allocentric spatial location encoding and recognition. Exp. Brain Res. 173 (4), 661–672.

Friston, K.J., Holmes, A., Poline, J.B., Price, C.J., Frith, C.D., 1996. Detecting activations in PET and fMRI: levels of inference and power. Neuroimage 4 (3 Pt 1), 223–235.

Frith, C.D., 2007. The social brain? Philos. Trans. R. Soc. Lond. B Biol. Sci. 362 (1480), 671–678.

Frith, U., Frith, C.D., 2003. Development and neurophysiology of mentalizing. Philos. Trans. R. Soc. Lond. B Biol. Sci. 358 (1431), 459–473.

Frith, C.D., Frith, U., 2006. How we predict what other people are going to do. Brain Res. 1079 (1), 36–46.

Gallagher, H.L., Frith, C.D., 2003. Functional imaging of ‘theory of mind’. Trends Cogn. Sci. 7 (2), 77–83.

Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G., 1996. Action recognition in the premotor cortex. Brain 119 (Pt 2), 593–609.

Gallese, V., Keysers, C., Rizzolatti, G., 2004. A unifying view of the basis of social cognition. Trends Cogn. Sci. 8 (9), 396–403.

Gauthier, I., Tarr, M.J., Anderson, A.W., Skudlarski, P., Gore, J.C., 1999. Activation of the middle fusiform ‘face area’ increases with expertise in recognizing novel objects. Nat. Neurosci. 2 (6), 568–573.

Gauthier, I., Skudlarski, P., Gore, J.C., Anderson, A.W., 2000. Expertise for cars and birds recruits brain areas involved in face recognition. Nat. Neurosci. 3 (2), 191–197.

Gazzola, V., Rizzolatti, G., Wicker, B., Keysers, C., 2007. The anthropomorphic brain: the mirror neuron system responds to human and robotic actions. Neuroimage 35 (4), 1674–1684.

Gobbini, M.I., Koralek, A.C., Bryan, R.E., Montgomery, K.J., Haxby, J.V., 2007. Two takes on the social brain: a comparison of theory of mind tasks. J. Cogn. Neurosci. 19 (11), 1803–1814.

Golby, A.J., Poldrack, R.A., Brewer, J.B., Spencer, D., Desmond, J.E., Aron, A.P., et al., 2001. Material-specific lateralization in the medial temporal lobe and prefrontal cortex during memory encoding. Brain 124 (Pt 9), 1841–1854.

Grafton, S.T., Mazziotta, J.C., Woods, R.P., Phelps, M.E., 1992. Human functional anatomy of visually guided finger movements. Brain 115 (Pt 2), 565–587.

Grafton, S.T., Arbib, M.A., Fadiga, L., Rizzolatti, G., 1996. Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. Exp. Brain Res. 112 (1), 103–111.

Grezes, J., Decety, J., 2002. Does visual perception of object afford action? Evidence from a neuroimaging study. Neuropsychologia 40 (2), 212–222.

Grezes, J., Fonlupt, P., Bertenthal, B., Delon-Martin, C., Segebarth, C., Decety, J., 2001. Does perception of biological motion rely on specific brain regions? Neuroimage 13 (5), 775–785.

Grezes, J., Frith, C., Passingham, R.E., 2004. Brain mechanisms for inferring deceit in the actions of others. J. Neurosci. 24 (24), 5500–5505.

Grossman, E.D., Blake, R., 2001. Brain activity evoked by inverted and imagined biological motion. Vis. Res. 41 (10–11), 1475–1482.

Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., et al., 2000. Brain areas involved in perception of biological motion. J. Cogn. Neurosci. 12 (5), 711–720.

Gusnard, D.A., Raichle, M.E., 2001. Searching for a baseline: functional imaging and the resting human brain. Nat. Rev. Neurosci. 2 (10), 685–694.

Hamilton, A.F., Grafton, S.T., 2007. The motor hierarchy: from kinematics to goals and intentions. In: Haggard, P., Rosetti, Y., Kawato, M. (Eds.), Attention and Performance, p. 22.

Heider, F., Simmel, M., 1944. An experimental study of apparent behavior. Am. J. Psychol. 57, 243–259.

Herry, C., Bach, D.R., Esposito, F., Di Salle, F., Perrig, W.J., Scheffler, K., et al., 2007. Processing of temporal unpredictability in human and animal amygdala. J. Neurosci. 27 (22), 5958–5966.

Hoistad, M., Barbas, H., 2008. Sequence of information processing for emotions through pathways linking temporal and insular cortices with the amygdala. Neuroimage 40 (3), 1016–1033.

Horan, W.P., Nuechterlein, K.H., Wynn, J.K., Lee, J., Castelli, F., Green, M.F., 2009. Disturbances in the spontaneous attribution of social meaning in schizophrenia. Psychol. Med. 39 (4), 635–643.

Howard, R.J., Brammer, M., Wright, I., Woodruff, P.W., Bullmore, E.T., Zeki, S., 1996. A direct demonstration of functional specialization within motion-related visual and auditory cortex of the human brain. Curr. Biol. 6 (8), 1015–1019.

Huettel, S.A., 2006. Behavioral, but not reward, risk modulates activation of prefrontal, parietal, and insular cortices. Cogn. Affect. Behav. Neurosci. 6 (2), 141–151.

Iacoboni, M., Dapretto, M., 2006. The mirror neuron system and the consequences of its dysfunction. Nat. Rev. Neurosci. 7 (12), 942–951.

Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C., Rizzolatti, G., 1999. Cortical mechanisms of human imitation. Science 286 (5449), 2526–2528.

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J.C., Rizzolatti, G., 2005. Grasping the intentions of others with one's own mirror neuron system. PLoS Biol. 3 (3), e79.

Jabbi, M., Swart, M., Keysers, C., 2007. Empathy for positive and negative emotions in the gustatory cortex. Neuroimage 34 (4), 1744–1753.

Johansson, G., 1973. Perception of biological motion and a model for its analysis. Percept. Psychophys. 14, 201–211.

Johnson, S.C., 2003. Detecting agents. Philos. Trans. R. Soc. Lond. B Biol. Sci. 358 (1431), 549–559.

Johnson, S.C., Booth, A., O'Hearn, K., 2001. Inferring the goals of a nonhuman agent. Cognitive Dev. 16, 637–656.

Johnson, S.C., Baxter, L.C., Wilder, L.S., Pipe, J.G., Heiserman, J.E., Prigatano, G.P., 2002. Neural correlates of self-reflection. Brain 125 (Pt 8), 1808–1814.

Josephs, O., Henson, R.N., 1999. Event-related functional magnetic resonance imaging: modelling, inference and optimization. Philos. Trans. R. Soc. Lond. B Biol. Sci. 354 (1387), 1215–1228.

Kana, R.K., Keller, T.A., Cherkassky, V.L., Minshew, N.J., Just, M.A., 2009. Atypical frontal–posterior synchronization of theory of mind regions in autism during mental state attribution. Soc. Neurosci. 4 (2), 135–152.

Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. J. Neurosci. 17 (11), 4302–4311.

Kim, H., Somerville, L.H., Johnstone, T., Alexander, A.L., Whalen, P.J., 2003. Inverse amygdala and medial prefrontal cortex responses to surprised faces. NeuroReport 14 (18), 2317–2322.

Kuhnen, C.M., Knutson, B., 2005. The neural basis of financial risk taking. Neuron 47 (5), 763–770.

Leslie, A.M., 1984. Spatiotemporal continuity and the perception of causality in infants. Perception 13 (3), 287–305.

Lou, H.C., Luber, B., Crupain, M., Keenan, J.P., Nowak, M., Kjaer, T.W., et al., 2004. Parietal cortex and representation of the mental self. Proc. Natl Acad. Sci. USA 101 (17), 6827–6832.

Maguire, E.A., 2001. Neuroimaging studies of autobiographical event memory. Philos. Trans. R. Soc. Lond. B Biol. Sci. 356 (1413), 1441–1451.

Maguire, E.A., Mummery, C.J., Buchel, C., 2000. Patterns of hippocampal–cortical interaction dissociate temporal lobe memory subsystems. Hippocampus 10 (4), 475–482.

Mar, R.A., Kelley, W.M., Heatherton, T.F., Macrae, C.N., 2007. Detecting agency from the biological motion of veridical vs animated agents. Soc. Cogn. Affect. Neurosci. 2 (3), 199–205.

Martin, A., Weisberg, J., 2003. Neural foundations for understanding social and mechanical concepts. Cogn. Neuropsychol. 20 (3–6), 575–587.

Martinez-Trujillo, J.C., Cheyne, D., Gaetz, W., Simine, E., Tsotsos, J.K., 2007. Activation of area MT/V5 and the right inferior parietal cortex during the discrimination of transient direction changes in translational motion. Cereb. Cortex 17 (7), 1733–1739.

Michotte, A., 1946. La perception de la causalite, etudes psychologiques vi. Institut superieur de philosophie, France.

Misaki, M., Matsumoto, E., Miyauchi, S., 2002. Dorsal visual cortex activity elicited by posture change in a visuo-tactile matching task. NeuroReport 13 (14), 1797–1800.

Ochsner, K.N., Knierim, K., Ludlow, D.H., Hanelin, J., Ramachandran, T., Glover, G., et al., 2004. Reflecting upon feelings: an fMRI study of neural systems supporting the attribution of emotion to self and other. J. Cogn. Neurosci. 16 (10), 1746–1772.

Olson, I.R., Plotzker, A., Ezzyat, Y., 2007. The Enigmatic temporal pole: a review of findings on social and emotional processing. Brain 130 (Pt 7), 1718–1731.

Paulus, M.P., Rogalsky, C., Simmons, A., Feinstein, J.S., Stein, M.B., 2003. Increased activation in the right insula during risk-taking decision making is related to harm avoidance and neuroticism. Neuroimage 19 (4), 1439–1448.

Pelphrey, K.A., Mitchell, T.V., McKeown, M.J., Goldstein, J., Allison, T., McCarthy, G., 2003. Brain activity evoked by the perception of human walking: controlling for meaningful coherent motion. J. Neurosci. 23 (17), 6819–6825.

Penny, W.D., Holmes, A.P., Friston, K.J., 2003. Random effects analysis. In: Frackowiak, R.S.J., Friston, K.J., Frith, C., Dolan, R., Price, C.J., Zeki, S., Ashburner, J., Penny, W.D. (Eds.), Human Brain Function. Academic Press.

Pessoa, L., Padmala, S., Morland, T., 2005. Fate of unattended fearful faces in the amygdala is determined by both attentional resources and cognitive modulation. Neuroimage 28 (1), 249–255.

Phillips, M.L., Young, A.W., Senior, C., Brammer, M., Andrew, C., Calder, A.J., et al., 1997. A specific neural substrate for perceiving facial expressions of disgust. Nature 389 (6650), 495–498.

Phillips, M.L., Williams, L.M., Heining, M., Herba, C.M., Russell, T., Andrew, C., et al., 2004. Differential neural responses to overt and covert presentations of facial expressions of fear and disgust. Neuroimage 21 (4), 1484–1496.

Pinkham, A.E., Penn, D.L., Perkins, D.O., Lieberman, J., 2003. Implications for the neural basis of social cognition for the study of schizophrenia. Am. J. Psychiatry 160 (5), 815–824.

Pinkham, A.E., Hopfinger, J.B., Ruparel, K., Penn, D.L., 2008. An investigation of the relationship between activation of a social cognitive neural network and social functioning. Schizophr. Bull. 34 (4), 688–697.

Preuschoff, K., Quartz, S.R., Bossaerts, P., 2008. Human insula activation reflects risk prediction errors as well as risk. J. Neurosci. 28 (11), 2745–2752.

Rao, H., Zhou, T., Zhuo, Y., Fan, S., Chen, L., 2003. Spatiotemporal activation of the two visual pathways in form discrimination and spatial location: a brain mapping study. Hum. Brain Mapp. 18 (2), 79–89.

Rauchs, G., Orban, P., Balteau, E., Schmidt, C., Degueldre, C., Luxen, A., et al., 2008. Partially segregated neural networks for spatial and contextual memory in virtual navigation. Hippocampus 18 (5), 503–518.

Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. Annu. Rev. Neurosci. 27, 169–192.

Rizzolatti, G., Fogassi, L., Gallese, V., 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. Nat. Rev. Neurosci. 2 (9), 661–670.

Rochat, P., Morgan, R., Carpenter, M., 1997. Young infants' sensitivity to movement information specifying social causality. Cognitive Dev. 12, 537–561.

Ruby, P., Decety, J., 2001. Effect of subjective perspective taking during simulation of action: a PET investigation of agency. Nat. Neurosci. 4 (5), 546–550.

Russell, T.A., Reynaud, E., Herba, C., Morris, R., Corcoran, R., 2006. Do you see what I see? Interpretations of intentional movement in schizophrenia. Schizophr. Res. 81 (1), 101–111.

Saarela, M.V., Hlushchuk, Y., Williams, A.C., Schurmann, M., Kalso, E., Hari, R., 2007. The compassionate brain: humans detect intensity of pain from another's face. Cereb. Cortex 17 (1), 230–237.

Salter, G., Seigal, A., Claxton, M., Lawrence, K., Skuse, D., 2008. Can autistic children read the mind of an animated triangle? Autism 12 (4), 349–371.

Santos, N.S., David, N., Bente, G., Vogeley, K., 2008. Parametric induction of animacy experience. Conscious. Cogn. 17 (2), 425–437.

Saxe, R., Xiao, D.K., Kovacs, G., Perrett, D.I., Kanwisher, N., 2004. A region of right posterior superior temporal sulcus responds to observed intentional actions. Neuropsychologia 42 (11), 1435–1446.

Schilbach, L., Wohlschlaeger, A.M., Kraemer, N.C., Newen, A., Shah, N.J., Fink, G.R., et al., 2006. Being with virtual others: neural correlates of social interaction. Neuropsychologia 44 (5), 718–730.

Schilbach, L., Wilms, M., Eickhoff, S.B., Romanzetti, S., Tepest, R., Bente, G., Jon Shah, N., Fink, G.R., Vogeley, K., 2009. Minds made for sharing: initiating joint attention recruits reward-related neurocircuitry. Journal of Cognitive Neuroscience 1–14. doi:10.1162/jocn.2009.21401.

Schlottmann, A., Surian, L., 1999. Do 9-month-olds perceive causation-at-a-distance? Perception 28 (9), 1105–1113.

Schultz, R.T., Grelotti, D.J., Klin, A., Kleinman, J., Van der Gaag, C., Marois, R., et al., 2003. The role of the fusiform face area in social cognition: implications for the pathobiology of autism. Philos. Trans. R. Soc. Lond. B Biol. Sci. 358 (1430), 415–427.

Schultz, J., Imamizu, H., Kawato, M., Frith, C.D., 2004. Activation of the human superior temporal gyrus during observation of goal attribution by intentional objects. J. Cogn. Neurosci. 16 (10), 1695–1705.

Schultz, J., Friston, K.J., O'Doherty, J., Wolpert, D.M., Frith, C.D., 2005. Activation in posterior superior temporal sulcus parallels parameter inducing the percept of animacy. Neuron 45 (4), 625–635.

Shulman, G.L., Ollinger, J.M., Linenweber, M., Petersen, S.E., Corbetta, M., 2001. Multiple neural correlates of detection in the human brain. Proc. Natl Acad. Sci. USA 98 (1), 313–318.

Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R.J., Frith, C.D., 2004. Empathy for pain involves the affective but not sensory components of pain. Science 303 (5661), 1157–1162.

Singer, T., Critchley, H.D., Preuschoff, K., 2009. A common role of insula in feelings, empathy and uncertainty. Trends Cogn. Sci. 13 (8), 334–340.

Skuse, D.H., Gallagher, L., 2009. Dopaminergic–neuropeptide interactions in the social brain. Trends Cogn. Sci. 13 (1), 27–35.

Small, D.M., Gregory, M.D., Mak, Y.E., Gitelman, D., Mesulam, M.M., Parrish, T., 2003. Dissociation of neural representation of intensity and affective valuation in human gustation. Neuron 39 (4), 701–711.

Somerville, L.H., Heatherton, T.F., Kelley, W.M., 2006. Anterior cingulate cortex responds differentially to expectancy violation and social rejection. Nat. Neurosci. 9 (8), 1007–1008.

Springer, K., Meier, Jo.A., Berry, D.S., 1996. Nonverbal bases of social perception: developmental change in sensitivity to patterns of motion that reveal interpersonal events. J. Nonverbal Behav. 20 (4), 199–211.

Stewart, J.A., 1984. Object motion and the perception of animacy. Paper presented at the Psychonomic Society Meeting.

Straube, T., Pohlack, S., Mentzel, H.J., Miltner, W.H., 2008. Differential amygdala activation to negative and positive emotional pictures during an indirect task. Behav. Brain Res. 191 (2), 285–288.

Tavares, P., Lawrence, A.D., Barnard, P.J., 2008. Paying attention to social meaning: an FMRI study. Cereb. Cortex 18 (8), 1876–1885.

Tomasello, M., Carpenter, M., Call, J., Behne, T., Moll, H., 2005. Understanding and sharing intentions: the origins of cultural cognition. Behav. Brain Sci. 28 (5), 675–691 discussion 691–735.

Tremoulet, P.D., Feldman, J., 2006. The influence of spatial context and the role of intentionality in the interpretation of animacy from motion. Percept. Psychophys. 68 (6), 1047–1058.

Vaina, L.M., Solomon, J., Chowdhury, S., Sinha, P., Belliveau, J.W., 2001. Functional neuroanatomy of biological motion perception in humans. Proc. Natl Acad. Sci. USA 98 (20), 11656–11661.

Van Overwalle, F., 2009. Social cognition and the brain: a meta-analysis. Hum. Brain Mapp. 30 (3), 829–858.

Van Overwalle, F., Baetens, K., 2009. Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. Neuroimage 48 (3), 564–584.

Vogeley, K., Bussfeld, P., Newen, A., Herrmann, S., Happe, F., Falkai, P., et al., 2001. Mind reading: neural mechanisms of theory of mind and self-perspective. Neuroimage 14 (1 Pt 1), 170–181.

Vogeley, K., May, M., Ritzl, A., Falkai, P., Zilles, K., Fink, G.R., 2004. Neural correlates of first-person perspective as one constituent of human self-consciousness. J. Cogn. Neurosci. 16 (5), 817–827.

Walter, H., Adenzato, M., Ciaramidaro, A., Enrici, I., Pia, L., Bara, B.G., 2004. Understanding intentions in social interaction: the role of the anterior paracingulate cortex. J. Cogn. Neurosci. 16 (10), 1854–1863.

Whalen, P.J., 2007. The uncertainty of it all. Trends Cogn. Sci. 11 (12), 499–500.

Whalen, P.J., Bush, G., McNally, R.J., Wilhelm, S., McInerney, S.C., Jenike, M.A., et al., 1998. The emotional counting Stroop paradigm: a functional magnetic resonance imaging probe of the anterior cingulate affective division. Biol. Psychiatry 44 (12), 1219–1228.

Wheatley, T., Milleville, S.C., Martin, A., 2007. Understanding animate agents: distinct roles for the social network and mirror system. Psychol. Sci. 18 (6), 469–474.

Zahn, R., Moll, J., Krueger, F., Huey, E.D., Garrido, G., Grafman, J., 2007. Social concepts are represented in the superior anterior temporal cortex. Proc. Natl Acad. Sci. USA 104 (15), 6430–6435.

When seeing does not lead to feeling: Absent neural tracking of subjective animacy experience in high-functioning autism

Bojana Kuzmanovic[a,b], MS, Leonhard Schilbach[b,c], MD, Alexandra L. Georgescu[b], MS, Hanna Kockler[b], MD, Natacha S. Santos[b], MS, N. Joni Shah[d], PhD, Gary Bente[e], PhD, Gereon R. Fink[f,g], MD, & Kai Vogeley[b,f] , MD, PhD.

[a] Institute of Neuroscience and Medicine – Ethics in the Neurosciences (INM-8), Research Center Juelich, Germany;

[b] Department of Psychiatry and Psychotherapy, University Hospital Cologne, Germany;

[c] Max-Planck Institute for Neurological Research, Cologne, Germany;

[d] Institute of Neuroscience and Medicine – Medical Imaging Physics (INM-4), Research Center Juelich, Germany;

[e] Department of Social Psychology and Media Psychology, University of Cologne, Germany;

[f] Institute of Neuroscience and Medicine – Cognitive Neurology Section (INM-3), Research Center Juelich, Germany;

[g] Department of Neurology, University Hospital Cologne, Germany.

Running title: **When seeing does not lead to feeling**

Keywords: animacy, high-functioning autism, fMRI, amygdala, dmPFC, feature-based processing.

Article body word length: 3960; abstract word length: 200.

Corresponding author:

Bojana Kuzmanovic

Forschungszentrum Juelich GmbH, INM-8, 52425 Juelich, DE

Tel 0049 2461 615237, Fax 0049 2461 612950, E-Mail b.kuzmanovic@fz-juelich.de.

Abstract

In individuals with high-functioning autism (HFA), the interpretation of social stimuli is assumed to rely more on feature-based cognitive strategies than on intuitive heuristics. To examine this, we computed neural correlates of increasing animacy in dynamic geometric shapes based on physical features and on subjective perceptions.

13 HFA adults and 13 matched controls rated the “person-likeness” of stimuli with increasingly interactive movement patterns during fMRI. Parametric modulations of neural responses to stimuli were analysed by using i) *subjective*, i.e. rating-related, and ii) *objective*, i.e. movement-related measures of animacy.

In controls relative to HFA, increasing *subjective animacy* correlated more strongly with activity in amygdala and dorsal medial prefrontal cortex (mPFC) associated with enhanced salience and mentalizing. In contrast, in both groups *objective animacy* was correlated with activity in superior temporal gyrus and ventral mPFC related to processing and evaluating meaningful movements. Furthermore, the more ratings correlated with stimulus properties, the stronger was the involvement of temporo-parietal regions in controls, relative to HFA.

These results confirm specific differences in cognitive strategies between HFA and controls by suggesting that in HFA feature-based classification of social stimuli is relatively intact, while more complex processes related to subjectively experienced salience and mind attribution are absent.

Introduction

Being able to spontaneously and effortlessly apprehend other minds is a skill we take for granted, which makes it difficult to imagine that it may not be readily available. Autism spectrum disorders, however, are characterized by such impairment in mind perception and understanding. In particular, adults with high-functioning autism (HFA) demonstrate a remarkable discrepancy between intact non-social cognitive capacities and impaired processing of social information (Klin and Jones, 2006). Thus, by applying compensatory cognitive strategies that rely more on feature-based processing, individuals with HFA may nonetheless be able to correctly classify and interpret social stimuli observed in experimental settings (Klin et al., 2003; Schilbach et al., 2011). However, due to reduced salience and intrinsic significance of social cues and the stronger focus on physical properties of stimuli in HFA (Klin et al., 2003), this performance may be accompanied by differential emotional and/or cognitive responses and hence altered subjective experience (Kuzmanovic et al., 2011). Within the ability to spontaneously grasp social meanings, animacy (i.e., the interpretation of entities as mindful agents) represents a constitutive component. This phenomenon of mind attribution is not restricted to living beings but may also occur when perceiving dynamically moving geometric figures (Heider and Simmel, 1944). Using such figures to evoke animacy impressions, neuroimaging studies have revealed the recruitment of brain regions associated with different aspects of social cognition (Castelli et al., 2000; Gobbini et al., 2007; Santos et al., 2010; Schultz et al., 2003; Tavares et al., 2008; Wheatley et al., 2007). Moreover, animacy perception tasks have proven to be sensitive to differences in the frequency of ‘mentalistic’ interpretations between HFA and controls, despite comparable performances on “classical”, explicit mentalizing tasks (Abell et al., 2000; Klin, 2000), as well as to reduced neural responses to animated stimuli in HFA in relevant social neural regions (Castelli et al., 2002; Spengler et al., 2010).

In the present study we used an established functional magnetic resonance imaging (fMRI) paradigm drawing upon animacy perception in moving geometric figures (Santos et al., 2010). In contrast to previous research, stimuli in this paradigm systematically varied as to parametrically increase the impression of animacy (see Figure 1). This was achieved by modulating interactive movements between two spheres, which have been demonstrated to be crucial for the perception of animacy (Santos et al., 2010). In addition to this objective measure of animacy, all stimuli were rated on a trial-by-trial basis with respect to the subjectively perceived "person-likeness". Consequently, this procedure provided both exogenous and endogenous measures for the same task. Effects of *objective* (stimulus-related) and *subjective* (rating-related) *animacy* were compared between HFA and controls. We hypothesized that basic perceptual, stimulus-driven processes used for feature-based classification of social cues could be largely intact in HFA (Klin and Jones, 2006), while profound differences should exist with regard to subjectively experienced salience and mind attribution, that have been previously associated with the amygdala (Pessoa, 2008; Robinson et al., 2010) an the dorsomedial prefrontal cortex (dmPFC) (Amodio and Frith, 2006). In addition, the correlation between objective stimuli properties and their subjective ratings in each participant – referred to as the *subjective-objective fit* (SOF) – allowed to investigate whether inter-individual differences regarding the propensity to recognize animacy were related to the same neural regions in HFA and controls.

Methods

Participants

Thirteen HFA participants were compared to 13 controls matched for gender, age, years of education and IQ (see Table 1). HFA participants were diagnosed and recruited in the Autism Outpatient Clinic at the Department of Psychiatry and Psychotherapy, University Hospital

Cologne, Germany. Diagnoses were made independently by two trained physicians corresponding to ICD-10 criteria and supplemented by an extensive neuropsychological assessment. Included were patients with the diagnoses childhood autism (F84.0) and Asperger syndrome (F84.5) with an at least average IQ and thus with a high level of intellectual functioning. Except for three participants who were taking antidepressants (1x Zoloft 50mg/day, 2x Citalopram 20mg/day) and reported episodes of depression, the HFA sample was free of psychotropic medication. As depression is a common co-morbidity in HFA (Lehnhardt et al., 2011; Stewart et al., 2006), they were not excluded although this resulted in a significant difference in the Beck Depression Inventory (BDI) score (Beck and Steer, 1987) between HFA and controls (see Table 1). To control for depression symptoms, BDI was included as a covariate in all data analyses (see Data Analyses). Furthermore, in accordance with the clinical diagnoses, there were significant differences in the Autism Spectrum Quotient (AQ) (Wheelwright et al., 2006) between HFA and controls (see Table 1).

Control participants were recruited online by addressing students and employees of the University of Cologne and the Research Center Juelich. They had no history of neurological or psychiatric disorders, and did not take any psychotropic medication. For matching purposes, intelligence in both groups was assessed by a German multiple choice vocabulary test (“Wortschatztest”, WST) (Lehrl et al., 1995; Schmidt and Metzler, 1992). After complete description of the study to the participants, written informed consent was obtained. The study was conducted with the approval of the local ethics committee.

Experimental procedure

Stimuli consisted of short video clips in which the basic scenery included two spheres (see Figure 1): one crossing the scene horizontally in the background (sphere 1), and the other placed in the front (sphere 2). Previous research has demonstrated that the perception of animacy can be induced by movements indicating “approach” and “responsiveness” (Santos et al., 2010). Thus, the movement of sphere 1 was either steady or contained an interruption followed by a movement towards the other sphere thereby creating the impression of an approach. Sphere 2 either remained static or moved towards sphere 1 thereby indicating responsiveness. These movement characteristics were combined to four possible stimulus categories with an increasing amount of objective animacy (see Figure 1). Other stimulus characteristics such as the laterality or the vertical perspective of the scene were balanced across the four stimulus categories, as they have been shown to not significantly modulate the subjective experience of animacy (Santos et al., 2010). Furthermore, the time delay of the approach varied between 0 and 1s, but did not have any behavioral effect (Santos et al., 2010). Because of the use of geometric figures embedded in a maximally simplified setting, that do not represent social cues such as faces or complex interactive scenarios, the use of eye tracking was not indispensable to control for gaze behavior between the groups (Zwickel et al., 2010). The total stimulus duration varied between 2 and 5.7s, depending on movement events included. In total, 104 stimuli were presented in a randomized order with an intertrial jitter of 2-4s in two sessions, each lasting 6.25min, using Presentation software (Version 12.2, Neurobehavioral Systems, Inc). Participants were asked to evaluate each stimulus with regard to how “person-like” they experienced the movement of the spheres on a four-point rating scale ranging from 1 = physical to 4 = person-like. They were instructed to respond at the end of the stimulus presentation via a LUMItouch keypad (Photon Control Inc). A Magnetom Trio 3T whole body scanner (Siemens AG, Medical Solutions) was used to acquire fMRI data with a T2*-weighted gradient echo planar imaging (EPI) sequence (TR = 2500 ms, TE = 30 ms, 40 axial slices aligned parallel to the AC-PC plane, flip angle = 90°, voxel size: 3.1x3.1x3 mm, 200 mm FOV, 64x64 matrix, 147 volumes per session). Three additional volumes were collected and discarded at the beginning of each session to allow for magnetic saturation.

Behavioral data analyses

All analyses were done using SPSS (PASW Statistics 18) and included BDI as a covariate to control for differences in reported depression symptoms between groups. The effect of stimulus categories on ratings as well as group differences were tested by a mixed ANOVA with group (HFA vs. control) as a between-subject factor and stimulus category (codes 1 to 4 for stimulus categories, see Figure 1) as a within-subject factor. Additionally, Pearson correlation coefficients (*r*) were computed between ratings of each participant and correspondent stimulus categories resulting in the *subjective-objective fit* (SOF). Group differences in SOF were tested by a univariate ANOVA. Finally, in order to document whether the groups differed in the frequency with which they chose the four possible response options, a second mixed ANOVA was conducted with group as a between-subject factor and response option (ratings on a four-point-scale and missing responses) as a within-subject factor.

fMRI data analyses

FMRI data were preprocessed and analyzed using MATLAB 7.1 (The MathWorks, Inc) and SPM8 (The Wellcome Trust Center for Neuroimaging). The EPI images were corrected for head movements using realignment and unwarping, normalized to the Montreal Neurological Institute (MNI) reference space using the unified segmentation function and spatially smoothed with an 8mm FWHM Gaussian kernel.

In all single subject analyses, conditions were modeled using a boxcar reference vector convolved with the canonical hemodynamic response function and its time derivative. Onsets for events of interests were set at 1s before the end of each video clip with a 1s duration. Thus, the analyses focused only on the time window of the last second of the stimuli where the interactive movements were completed and could be evaluated by participants. In so doing, the duration of events of interest as well as the complexity of the enclosed movement were kept constant as the last second was exactly the same across all stimuli (sphere 1 exits the scene, see Figure 1). Low-frequency signal drifts were filtered using a cutoff of 128s. Single subject contrasts were fed into group analyses employing a random-effects model. All models included participants' BDI scores as a covariate in order to control for depression symptoms. On the group level, effects are reported as significant at $p<.05$, corrected for multiple comparisons at the cluster level ($p_{\text{FWE-corr}}$) with $p<.001$ at the voxel level. Functional activations were anatomically localized by using the brain atlas by Duvernoy (Duvernoy, 1999) and the SPM anatomy toolbox, version 1.7 (Eickhoff et al., 2007). Group activation maps were superimposed on the canonical MNI single-subject T1-weighted brain of SPM8. For the comparison of neural correlates of animacy perception between HFA and controls three types of analyses were performed. The first set of analyses focused on brain regions where the activity correlated with increasing *subjective animacy*. Using ratings of each participant for parametric modulation of his or her general neural response to the stimuli, we investigated where in the brain the neural signal correlated with the subjective experience of animacy, irrespective of stimulus properties. Trials with missing responses were modeled on a separate regressor. Additionally, in order to investigate whether subjective animacy accounted for unique variance, an upgraded model was specified including first objective and second subjective animacy as parametric regressors.

In the second set of analyses, the variation of animacy was operationalized objectively in accordance with systematic variations of stimulus properties. Here, codes for the four stimulus categories (see Figure 1) representing *objective animacy* were used for the parametric modulation of the general neural response to the stimuli.

Third, the groups were compared with respect to general processing of the stimulus material – i.e. disregarding objective or subjective animacy levels, with the SOF of each participant as a covariate. Here, we tested whether the general processing of the stimuli differed for participants with varying propensity to recognize animacy-relevant movement patterns.

Results

Behavioral results

The ANOVA focusing on the effects of stimulus category on ratings did not reveal a significant main effect of group (*F*(1,23)=.41, *p*=.526), nor a significant interaction between group and stimulus category (*F*(2.2,49.5)=1.69, *p*=.193; see Figure 2). Thus, controls and HFA participants did not differ in their rating of stimuli. There was a significant main effect of stimulus category on ratings (*F*(2.2,49.5)=28.49, *p*=.000) indicating that across groups, stimuli were rated as more person-like when they included increasingly more animacy inducing movement patterns. This finding supports paradigm validity since it demonstrates that the stimuli indeed induced a parametric increase in animacy perception.

The ANOVA comparing the groups with regard to SOF did not reveal a significant difference (*F*(1,23)=3.12, *p*=.091). On average, both groups showed a positive correlation between the subjective and the objective animacy (HFA: mean *r*=.56, *s*=.24; controls: mean *r*=.67, *s*=.17), providing further evidence that the stimuli affected the animacy ratings in the predicted manner across both groups.

Finally, the ANOVA focusing on response frequencies did not reveal any group differences either. There was neither a significant main effect of group (*F*(1,24)=1.00, *p*=.327) nor a significant interaction between group and response option (*F*(2.1,51.2)=.57, *p*=.582). Thus, by showing that response frequencies of HFA and control participants were comparable, these groups could be compared with regard to the parametric modulation of the BOLD-response by individual ratings.

fMRI results

The increase of neural activation with increasing *subjective animacy* experience was stronger in the control group compared to the HFA group in the dmPFC and the amygdala mainly located in the basolateral complex (Amunts et al., 2005) (see Table 2A for complete results and Figure 3A). There were no significant results for the reverse contrast (HFA > controls) or for the conjunction testing for common effects across both groups. Simple main effects of increasing subjective animacy revealed significant results for the control group (listed in Table 2A), but not for the HFA group. Furthermore, by including both objective and subjective animacy as parametric regressors in a supplementary analysis we tested whether subjective animacy accounted for different variance to that accounted for by varying stimulus properties. By using the effect of group difference in increasing subjective animacy reported in Table 2A as an inclusive mask, this upgraded model could replicate the prior results for controls > HFA, although at a more liberal statistical threshold (p<.005, uncorrected): right posterior insula (x=36, y=-18, z=-2, T=3.78, cluster size=150) extending into the right STG (x=52, y=-10, z=0, T=3.66), left STG (x=-52, y=-12, z=4, T=3.60, cluster size=110), left anterior insula (x=-32, y=4, z=-10, T=4.04, cluster size=109) extending into the temporal pole (x=-34, y=6, z=-22, T=3.05), left hippocampus (x=-34, y=-14, z=-18, T=3.70, cluster size=82), and the right hippocampus (x=22, y=-8, z=-32, T=3.56, cluster size=48) extending into the amygdala (x=24, y=-6, z=-18, T=2.69). Thus, there was unique variance accounted for by the subjective animacy despite the positive correlation between subjective and objective animacy in both groups.

There were no significant differences between the HFA and the control group in the parametric modulation of the neural response to stimuli by increasing *objective animacy* (controls > HFA, HFA > controls). Instead, the conjunction revealed a common neural network across both groups correlating with increasing objective animacy including the ventromedial PFC (vmPFC) and the bilateral rolandic operculum extending into the superior temporal gyrus (STG, see Table 3). The simple main effects of increasing objective animacy were calculated for the control and the HFA group, respectively, and are listed in Table 3. These results show that the control group demonstrated neural modulation by increasing objective animacy in a more extended network than the HFA group.

Finally, including the *subjective-objective fit* (SOF) of every participant as a covariate of the general neural response to stimuli revealed significant differences between the groups. Control participants with a greater SOF demonstrated a greater involvement of the left superior temporal sulcus (STS), superior frontal gyrus, and the right angular gyrus corresponding to the temporo-parietal junction (TPJ) as compared to HFA participants (see Table 2A and Figure 3B). There were no significant results for the reverse contrast (HFA > controls) or when computing the conjunction across the groups. As evident from the scatter charts provided in Figure 3B, there was one outlier within the HFA group with a very low SOF value (*r*=-0.03). However, we could replicate the results also under exclusion of the correspondent participant (STS: x=-56, y=-24, z=-6, *T*=7.77, cluster size=157; superior frontal gyrus: x=-16, y=32, z=48, *T*=5.35, cluster size=200; and angular gyrus: x=42, y=-60, z=32, *T*=5.00, cluster size=218). There were no significant simple main effects for the inter-individual correlation between the SOF and the general stimulus processing for either of the two groups.

Discussion

Depending on whether the neural responses to stimuli were correlated with *subjective* or *objective animacy* (within-subject level), or with the *subjective-objective fit* (SOF; between-subject level), comparisons between the HFA and the control group revealed divergent results. Significant group differences occurred in neural correlates of subjectively experienced animacy, although stimulus-driven neural responses and behavioral stimulus ratings were comparable. Thus, these findings suggest that classification of social cues based on stimulus properties was similar in both groups, while more complex responses beyond the perceptual analysis differed. Additionally, group differences occurred also with respect to neural correlates of inter-individual differences in SOF indicating the propensity to recognize animacy-relevant movement patterns.

Given that the task was designed to prompt social cognition, our general result pattern may be interpreted in two ways. First, the absence of a differential recruitment of brain areas associated with social cognition for subjective animacy in HFA may have occurred because the applied stimuli were unable to evoke social processing in a similar way as they did in neurotypical individuals. Supporting this explanation, individuals with HFA have been shown not to attend to socially relevant details of complex scenes indicating a reduced salience of social cues (Klin et al., 2003). Importantly, the lack of group differences in accuracy and missing responses in our study nevertheless demonstrated that in this simplified setting HFA participants were able to recognize animacy cues and were equally motivated to perform the task.

Second, due to the assumed impairment of social cognition in autism, individuals with HFA may have developed compensatory strategies based on a more tight analyses of physical stimulus properties as their integrative physical reasoning is not impaired (Klin and Jones, 2006). This possibility accounts for the observed modulatory effect of objective, i.e. stimulus-related, but not of subjective animacy on general stimulus processing in the HFA group. Within such a ‘strategic’ analysis of stimuli based on physical properties, only differences in physical properties themselves, but not in different outcomes of their appraisal need to be related to differences in neural activity. Notably, the two interpretations are not mutually exclusive, but may interact in the sense that a decreased predisposition for the salience of social cues has an impact on the development of social cognitive skills and possible compensatory strategies (Klin et al., 2003; Senju, 2011).

Beyond this general interpretation, the specific brain regions differentially involved during animacy processing should be considered with regard to their functional roles. One of the brain regions that more strongly correlated with increasing *subjective animacy* in controls as compared to HFA was the amygdala bilaterally. Serving as a highly interconnected node within multiple neural networks, the amygdala plays a central role in detecting salient sensory input (Pessoa, 2008; Robinson et al., 2010) and more specifically in recognizing and experiencing moving geometrical shapes as being animated (Castelli et al., 2002; Martin and Weisberg, 2003; Santos et al., 2010; Schultz et al., 2003; Tavares et al., 2008; Wheatley et al., 2007). Particularly the basolateral complex of the mammalian amygdala represents the primary input site where the majority of subcortical and cortical afferents such as visual information converge (Ball et al., 2007; Etkin et al., 2004). The close relationship between its activity and the animacy content of visual stimuli in controls confirm that in humans, too, the basolateral complex is a strong candidate for a subregion of the amygdala which is responsive to increased salience of sensory input.

The greater recruitment of the bilateral amygdala with increasing subjective animacy in controls as compared to HFA provides direct empirical support for the amygdala theory of autism, which proposes a specific dysfunction of this region (Baron-Cohen et al., 2000). Most of the evidence for this theory is indirect and relates to anatomical variations of the amygdala or to decreased amygdala involvement in autism when processing social nonverbal cues (Baron-Cohen et al., 1999; Critchley et al., 2000). However, none of these studies demonstrated a relationship between trial-to-trial task performance and amygdala activation. Thus, our findings provide first-time evidence that the evaluation of social stimuli in HFA does not rely on the differential involvement of the amygdala to the same extent as in controls, possibly because the presented stimuli conveyed relatively less social meaning resulting in a decreased subjectively experienced salience.

Furthermore, the increase of activity in the dmPFC with increasing subjective animacy experience was significantly stronger in controls than in HFA participants. As it plays a central role in classical mentalizing tasks (Amodio and Frith, 2006) and has been specifically involved in perceiving animacy of moving geometric figures (Castelli et al., 2002; Schultz et al., 2003; Tavares et al., 2008; Wheatley et al., 2007), the involvement of this region might be associated with mind attribution elicited by increasingly interactive movement patterns. Difficulties in mentalizing are constitutive for autism spectrum disorders and reduced dmPFC activity has been demonstrated in previous imaging studies focusing on animacy perception (Castelli et al., 2002) and 'mentalistic' story comprehension (Happe et al., 1996). Furthermore, the lack of modulation of dmPFC activation by increasing animacy ratings in HFA is in accordance with less frequent interpretations of interactively moving geometric figures in terms of mental states (Abell et al., 2000; Castelli et al., 2002; Klin, 2000). Thus, the absence of a differential involvement of the dmPFC provides further evidence for a different cognitive style in HFA that may be reactive to different stimulus properties, but does not imply mind attributions evoked by increasingly animated stimuli in neurotypical individuals.

In contrast, when focusing on *objective animacy*, i.e. on increasingly interactive movement patterns of the stimuli, there were no significant differences between the HFA and the control group. In both groups neural activity in the vmPFC and the bilateral rolandic operculum extending into the STG increased with increasing objective animacy. The STG has been demonstrated to be specifically associated with identification of objective movement characteristics, such as the amount of interactivity between two moving geometrical figures (Schultz et al., 2005). In general, this region seems to respond to animacy-inducing movement of objects (Santos et al., 2010; Schultz et al., 2003; Wheatley et al., 2007). Thus, its common involvement in both the HFA and the control group might represent a feature-based processing which depends on exogenous characteristics of stimuli, but is not directly related to endogenous responses, which depend on subjective appraisal beyond basic perception. Furthermore, these encoded features have to be integrated into an evaluative judgment that reflects internal values based on experiential learning, a process that has been specifically associated with the vmPFC (Phan et al., 2004; Zysset et al., 2003). Thereby, vmPFC might operate in a top-down manner to modulate the unfolding stimulus representation in the STG (Bar et al., 2006). Following this line of interpretation, the feature-based and top-down guided analysis of stimulus properties does not seem to be impaired in HFA which explains the comparable behavioral performance between the two groups.

Finally, we found interesting differences between groups when considering the covariance of the *SOF*, i.e. the fit between subjective and objective animacy, and the activity in the left STS, left superior frontal gyrus and right TPJ. In these brain regions, the activity was more strongly correlated with SOF in controls than in HFA participants, which indicates that they were engaged to a greater extent in neurotypical individuals with better propensities to recognize animacy-relevant movement patterns. The left STS and the right TPJ have previously been shown to be implicated in processing of biological motion (Blake and Shiffrar, 2007) and social inference (Van Overwalle and Baetens, 2009), respectively. The finding that the performance in animacy perception was not related to these regions in HFA is consistent with prior studies demonstrating less pronounced recruitment of the STS and TPJ in HFA as compared to controls during animacy perception (Castelli et al., 2002; Lombardo et al., 2011; Spengler et al., 2010) and further supports the assumption of differential neural mechanisms underlying social cognition in HFA.

Acknowledgments

We thank all HFA participants for their interest and support, B. Elghahwagi and D. Krug for assistance with fMRI data acquisition and A. Jefferson for helpful discussions and proofreading. This work was supported by the Federal Ministry of Education and Research (Germany) [grant number 01GP0802; KV].

Financial disclosures

None of the authors of the present study has declared any biomedical financial interests or potential conflicts of interest.

References

Abell F, Happe F, Frith U. Do triangles play tricks? Attribution of mental states to animated shapes in normal and abnormal development. Journal of Cognitive Development 2000; 15: 1-20.

Amodio DM, Frith CD. Meeting of minds: the medial frontal cortex and social cognition. Nat Rev Neurosci 2006; 7: 268-77.

Amunts K, Kedo O, Kindler M, Pieperhoff P, Mohlberg H, Shah NJ, et al. Cytoarchitectonic mapping of the human amygdala, hippocampal region and entorhinal cortex: intersubject variability and probability maps. Anat Embryol (Berl) 2005; 210: 343-52.

Ball T, Rahm B, Eickhoff SB, Schulze-Bonhage A, Speck O, Mutschler I. Response properties of human amygdala subregions: evidence based on functional MRI combined with probabilistic anatomical maps. PLoS One 2007; 2: e307.

Bar M, Kassam KS, Ghuman AS, Boshyan J, Schmid AM, Dale AM, et al. Top-down facilitation of visual recognition. Proc Natl Acad Sci U S A 2006; 103: 449-54.

Baron-Cohen S, Ring HA, Bullmore ET, Wheelwright S, Ashwin C, Williams SC. The amygdala theory of autism. Neurosci Biobehav Rev 2000; 24: 355-64.

Baron-Cohen S, Ring HA, Wheelwright S, Bullmore ET, Brammer MJ, Simmons A, et al. Social intelligence in the normal and autistic brain: an fMRI study. Eur J Neurosci 1999; 11: 1891-8.

Beck AT, Steer RA. Beck Depression Inventory - Manual. San Antonio: The Psychological Corporation, 1987.

Blake R, Shiffrar M. Perception of human motion. Annu Rev Psychol 2007; 58: 47-73.

Castelli F, Frith C, Happe F, Frith U. Autism, Asperger syndrome and brain mechanisms for the attribution of mental states to animated shapes. Brain 2002; 125: 1839-49.

Castelli F, Happe F, Frith U, Frith C. Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. Neuroimage 2000; 12: 314-25.

Critchley HD, Daly EM, Bullmore ET, Williams SC, Van Amelsvoort T, Robertson DM, et al. The functional neuroanatomy of social behaviour: changes in cerebral blood flow when people with autistic disorder process facial expressions. Brain 2000; 123 (Pt 11): 2203-12.

Duvernoy HM. The Human Brain: Surface, Three-Dimensional Sectional Anatomy with MRI, and Blood Supply. Wien/ New York: Springer, 1999.

Eickhoff SB, Paus T, Caspers S, Grosbras MH, Evans AC, Zilles K, et al. Assignment of functional activations to probabilistic cytoarchitectonic areas revisited. Neuroimage 2007; 36: 511-21.

Etkin A, Klemenhagen KC, Dudman JT, Rogan MT, Hen R, Kandel ER, et al. Individual differences in trait anxiety predict the response of the basolateral amygdala to unconsciously processed fearful faces. Neuron 2004; 44: 1043-55.

Gobbini MI, Koralek AC, Bryan RE, Montgomery KJ, Haxby JV. Two takes on the social brain: a comparison of theory of mind tasks. J Cogn Neurosci 2007; 19: 1803-14.

Happe F, Ehlers S, Fletcher P, Frith U, Johansson M, Gillberg C, et al. 'Theory of mind' in the brain. Evidence from a PET scan study of Asperger syndrome. Neuroreport 1996; 8: 197-201.

Heider F, Simmel M. An experimental study of apparent behavior. Am. J. Psychol. 1944; 57: 243-259.

Klin A. Attributing social meaning to ambiguous visual stimuli in higher-functioning autism and Asperger syndrome: The Social Attribution Task. J Child Psychol Psychiatry 2000; 41: 831-46.

Klin A, Jones W. Attributing social and physical meaning to ambiguous visual displays in individuals with higher-functioning autism spectrum disorders. Brain Cogn 2006; 61: 40-53.

Klin A, Jones W, Schultz R, Volkmar F. The enactive mind, or from actions to cognition: lessons from autism. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 2003; 358: 345-60.

Kuzmanovic B, Schilbach L, Lehnhardt F-G, Bente G, Vogeley K. A matter of words: Impact of verbal and nonverbal information on impression formation in high-functioning autism. Research in Autism Spectrum Disorders 2011; 5: 604-613.

Lehnhardt FG, Gawronski A, Volpert K, Schilbach L, Tepest R, Huff W, et al. Autism spectrum disorders in adulthood: clinical and neuropsychological findings of Aspergers syndrome diagnosed late in life. Fortschr Neurol Psychiatr 2011; 79: 290-7.

Lehrl S, Triebig G, Fischer B. Multiple choice vocabulary test MWT as a valid and short test to estimate premorbid intelligence. Acta Neurologica Scandinavica 1995; 91: 335-45.

Lombardo MV, Chakrabarti B, Bullmore ET, Baron-Cohen S. Specialization of right temporo-parietal junction for mentalizing and its relation to social impairments in autism. Neuroimage 2011; 56: 1832-8.

Martin A, Weisberg J. Neural foundations for understanding social and mechanical concepts. Cogn Neuropsychol 2003; 20: 575-87.

Pessoa L. On the relationship between emotion and cognition. Nat Rev Neurosci 2008; 9: 148-58.

Phan KL, Taylor SF, Welsh RC, Ho SH, Britton JC, Liberzon I. Neural correlates of individual ratings of emotional salience: a trial-related fMRI study. Neuroimage 2004; 21: 768-80.

Robinson JL, Laird AR, Glahn DC, Lovallo WR, Fox PT. Metaanalytic connectivity modeling: delineating the functional connectivity of the human amygdala. Hum Brain Mapp 2010; 31: 173-84.

Santos NS, Kuzmanovic B, David N, Rotarska-Jagiela A, Eickhoff SB, Shah JN, et al. Animated brain: a functional neuroimaging study on animacy experience. Neuroimage 2010; 53: 291-302.

Schilbach L, Eickhoff SB, Cieslik EC, Kuzmanovic B, Vogeley K. Shall we do this together? Social gaze influences action control in a comparison group, but not in individuals with high-functioning autism. Autism 2011.

Schmidt KH, Metzler P. Wortschatztest (WST). Weinheim: Beltz Test GmbH, 1992.

Schultz J, Friston KJ, O'Doherty J, Wolpert DM, Frith CD. Activation in posterior superior temporal sulcus parallels parameter inducing the percept of animacy. Neuron 2005; 45: 625-35.

Schultz RT, Grelotti DJ, Klin A, Kleinman J, Van der Gaag C, Marois R, et al. The role of the fusiform face area in social cognition: implications for the pathobiology of autism. Philos Trans R Soc Lond B Biol Sci 2003; 358: 415-27.

Senju A. Spontaneous Theory of Mind and Its Absence in Autism Spectrum Disorders. Neuroscientist 2011.

Spengler S, Bird G, Brass M. Hyperimitation of actions is related to reduced understanding of others' minds in autism spectrum conditions. Biol Psychiatry 2010; 68: 1148-55.

Stewart ME, Barnard L, Pearson J, Hasan R, O'Brien G. Presentation of depression in autism and Asperger syndrome: a review. Autism 2006; 10: 103-16.

Tavares P, Lawrence AD, Barnard PJ. Paying attention to social meaning: an FMRI study. Cereb Cortex 2008; 18: 1876-85.

Van Overwalle F, Baetens K. Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. Neuroimage 2009; 48: 564-84.

Wheatley T, Milleville SC, Martin A. Understanding animate agents: distinct roles for the social network and mirror system. Psychol Sci 2007; 18: 469-74.

Wheelwright S, Baron-Cohen S, Goldenfeld N, Delaney J, Fine D, Smith R, et al. Predicting Autism Spectrum Quotient (AQ) from the Systemizing Quotient-Revised (SQ-R) and Empathy Quotient (EQ). Brain Research 2006; 1079: 47-56.

Zwickel J, White SJ, Coniston D, Senju A, Frith U. Exploring the building blocks of social cognition: spontaneous agency perception and visual perspective taking in autism. Soc Cogn Affect Neurosci 2010; 6: 564-71.

Zysset S, Huber O, Samson A, Ferstl EC, von Cramon DY. Functional specialization within the anterior medial prefrontal cortex: a functional magnetic resonance imaging study with human subjects. Neurosci Lett 2003; 335: 183-6.

Figures

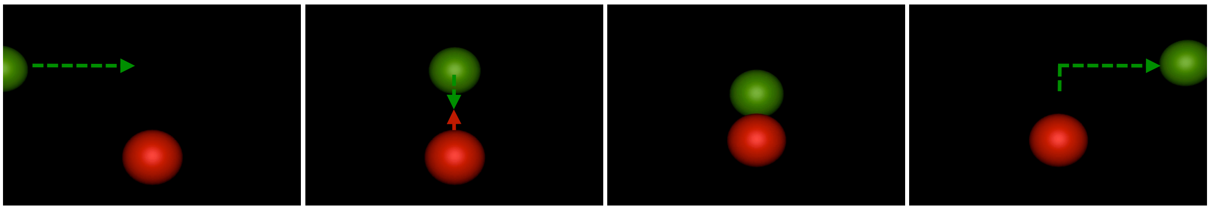

Figure 1 Four frames extracted out of a stimulus video clip containing “approach” and “responsiveness” with arrows indicating the pathways of movements. Across all stimuli, the beginning and the end were exactly the same showing a red sphere in the front and a green sphere entering the scene in the background, passing by and exiting the scene. The middle part of video clips was systematically varied across the four stimulus categories. In the least animated category, there was no additional action, i.e., the green sphere passed by without a stop or change in the direction and the green sphere showed no reaction (category 1, no approach-no responsiveness). In the most animated category, the green sphere stopped in front of the red one (frame 2) and approached it while the red sphere responded by moving towards the green sphere (frame 3; category 4, approach-responsiveness). Category 2 stimuli contained only responsiveness and category 3 stimuli only approach.

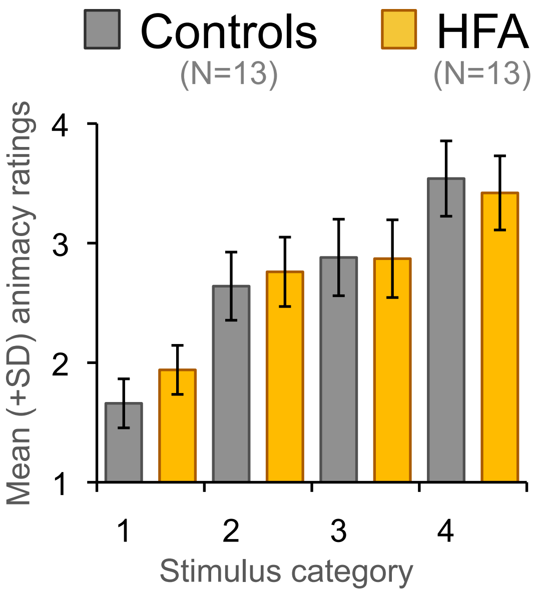

Figure 2 Mean animacy ratings of the four stimulus categories for the control and the HFA group. Comparable across groups, stimuli that included animacy-inducing movement patterns (approach and responsiveness) were perceived as more personal on a four-point rating scale (1=physical, 4 =personal).

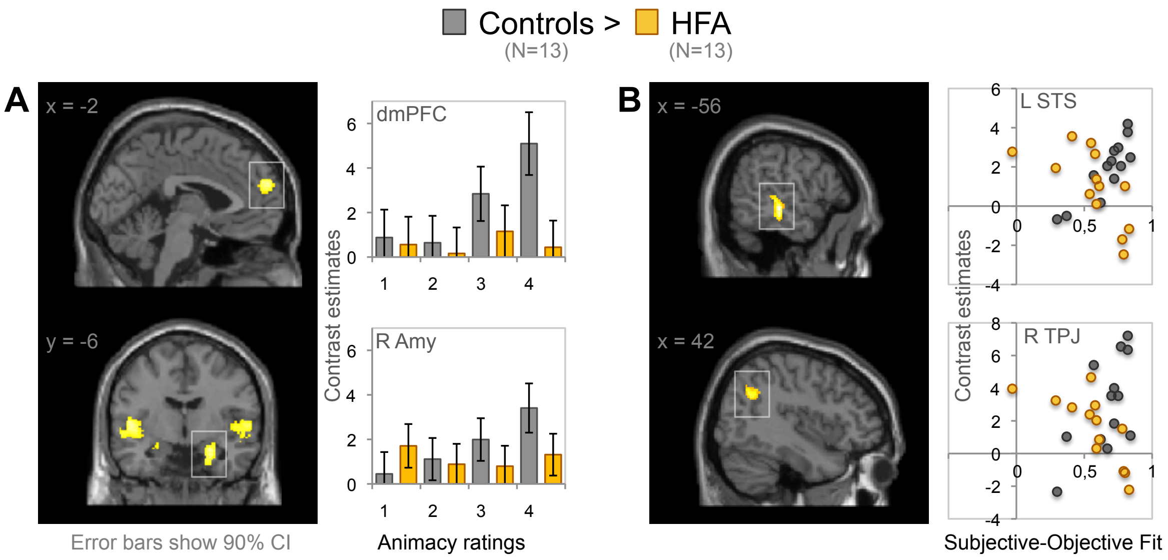

Figure 3 Group comparisons in within-subject (A) and between-subject (B) correlations between the BOLD signal and animacy-related measures. A) The effect of increasing *subjective animacy* (as indexed by participants' event-related ratings) that was significantly greater in the control than in the HFA 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: 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. B) Brain regions correlating with the subjective-objective fit (SOF, the fit between the ratings of a participant and the movement patterns of stimuli) to a significantly greater extent in the control than in the HFA group. Activation maps show group differences in the covariance of the general neural response to the stimuli, irrespective of animacy, and the SOF of each participant. For illustrative purposes, scatter charts showing the relation between the SOF and the contrast estimates of the significantly correlated neural regions are depicted: L STS: x=-56, y=-24, z=-6; R TPJ: x=42, y=-60, z=32. Activation maps were superimposed on the canonical MNI single-subject T1-weighted brain of SPM8. L, left; R, right; dmPFC, dorsomedial prefrontal cortex; Amy, Amygdala; STS, superior temporal sulcus; TPJ, temporoparietal junction.

Tables

Table 1 Demographic and neuropsychological data.

	HFA group		Control group			
	M	*s*	*M*	*s*	Statistics	
Gender (m:f)	8:5		8:5			
Age (years)	29.08	4.33	29.77	4.02	$t(24) = .42$	$p = .677$
Education (years)	16.96	3.99	19.50	3.10	$t(24) = 1.81$	$p = .083$
IQ	109.54	9.19	108.00	7.45	$t(24) = -.47$	$p = .643$
BDI[a]	9.92	8.14	3.46	3.89	$t(17.2) = -2.58$	$p = .016$*
AQ[a]	40.38	5.35	14.54	5.64	$t(24) = -11.99$	$p = .000$*

HFA, high-functioning autism; *M*, mean; *s*, standard deviation; m, male; f, female; BDI, Beck Depression Inventory; AQ, Autism Spectrum Quotient. *p<.05.

Table 2 Significant effects of within-subject (A) and between-subject (B) correlations between the BOLD signal and animacy related measures that revealed significant group differences: A) BOLD signals correlating with increasing subjective animacy; B) Covariation of the general neural processing of stimuli with the subjective-objective fit (SOF).

	Cluster-level		*Side*	*x*	*y*	*z*	*T*
	Size	$p_{FWE\text{-}corr}$					
A) INCREASING SUBJECTIVE ANIMACY							
Controls > HFA							
Insula (posterior)	628	.000	R	46	-12	2	5.24
Superior temporal gyrus			R	52	0	-12	4.70
Temporal pole			R	58	10	-8	3.40
Insula (posterior)	587	.000	L	-44	-10	-8	4.92
Rolandic operculum			L	-48	-8	6	4.92
Hippocampus			L	-28	-10	-16	4.21
Superior temporal gyrus			L	-56	-6	-4	3.94
Amygdala			L	-24	-6	-16	3.54
Dorsomedial prefrontal cortex	275	.004	L/R	-2	58	24	4.79
Hippocampus	272	.004	R	26	-8	-22	4.74
Amygdala			R	24	-6	-18	4.60
Insula (anterior)	269	.004	L	-36	8	-12	5.45
Temporal pole			L	-18	4	-22	4.03
Controls							
Rolandic operculum	4761	.000	L	-48	-8	-6	7.38
Fusiform gyrus			L	-28	-28	-22	6.04
Middle temporal gyrus			L	-62	-24	-6	5.87
Insula (posterior)			L	-36	6	-14	5.74
Temporal pole			L	-18	4	-22	5.57
Hippocampus			L	-28	-12	-16	5.48
Superior temporal gyrus			L	-54	-4	-4	5.37
Amygdala			L	-24	-6	-16	5.21
Dorsomedial prefrontal cortex	4055	.000	R/L	-2	58	24	6.28
Ventromedial prefrontal cortex			R/L	8	44	-18	6.08
Hippocampus	3033	.000	R	30	-12	-20	7.16
Superior temporal gyrus			R	58	-2	4	6.57
Insula (posterior)			R	48	-10	4	6.20
Amygdala			R	24	-6	-18	5.87
Temporal pole			R	58	8	-8	5.21
Insula (middle)			R	44	8	-4	4.10
Posterior cingulate gyrus	2319	.000	R/L	-4	-48	34	6.48
Middle cingulate gyrus			R/L	-2	-14	40	5.43
Paracentral lobule	397	.000	R/L	-2	-32	70	4.85
Angular gyrus	350	.001	L	-48	-74	30	4.82
B) COVARIANCE WITH THE SOF							
Controls > HFA							
Superior temporal sulcus	255	.003	L	-56	-24	-6	6.72
Middle temporal gyrus			L	-56	-24	-12	6.21
Superior frontal gyrus	230	.005	L	-16	30	50	5.40
Angular Gyrus	186	.015	R	42	-60	32	5.22

Table 3 Significant effects of increasing objective animacy.

	Cluster-level		*Side*	*x*	*y*	*z*	*T*
	Size	$p_{FWE\text{-}corr}$					
Conjunction: controls, HFA							
Ventromedial prefrontal cortex	427	.000	L	-4	50	-16	4.69
			R	6	52	-12	3.80
Rolandic operculum	333	.001	L	-54	-6	10	5.84
Superior temporal gyrus			L	-56	-6	6	5.68
Rolandic operculum	309	.002	R	56	-4	12	4.86
Superior temporal gyrus			R	56	-18	2	3.68
Controls							
Ventromedial prefrontal cortex	6261	.000	R/L	6	42	-16	8.73
Dorsomedial prefrontal gyrus			R/L	4	60	14	6.39
Fusiform gyrus	5187	.000	L	-26	-38	-16	7.12
Middle cingulate gyrus			R/L	-6	-32	42	6.84
Posterior cingulate gyrus			R/L	6	-48	26	6.41
Anterior calcarine sulcus			L	-16	-56	6	5.05
Rolandic operculum	3815	.000	L	-50	-6	4	7.70
Insula (anterior)			L	-34	8	-18	6.19
Insula (posterior)			L	-42	-6	-2	6.12
Superior temporal gyrus			L	-44	-16	-6	6.00
Middle temporal gyrus			L	-62	-20	-8	5.25
Hippocampus			L	-24	-10	-14	5.22
Amygdala			L	-24	-2	-24	4.88
Hippocampus	3564	.000	R	30	-12	-20	7.21
Superior temporal gyrus			R	58	-16	2	6.92
Temporal pole			R	48	4	-10	5.47
Middle temporal gyrus			R	64	-6	-22	5.22
Amygdala			R	28	-6	-18	4.97
Fusiform gyrus	402	.000	R	26	-64	-16	4.68
Angular gyrus	250	.006	L	-48	-74	32	4.16
Superior temporal gyrus	240	.008	L	-44	-30	12	4.77
Superior frontal gyrus	222	.011	L	-24	38	40	5.74
Parahippocampal gyrus	222	.011	R	22	-32	-14	5.09
Cerebellum			R	22	-44	-24	4.23
Anterior calcarine sulcus	203	.017	R	24	-54	6	4.57
HFA							
Superior temporal gyrus	1363	.000	R	46	-26	14	5.16
Insula (posterior)			R	40	-18	14	5.12
Rolandic operculum			R	58	0	12	4.97
Rolandic operculum	753	.000	L	-58	-4	9	6.42
Insula (posterior)			L	-34	-14	22	4.97
Superior temporal gyrus			L	-50	-22	12	3.40
Ventromedial prefrontal cortex	496	.000	L	-14	48	-4	5.62
			R	6	52	-12	3.80
Superior occipital gyrus	374	.001	R	16	-92	32	4.61
Middle occipital gyrus	225	.011	L	-20	-82	16	4.40
Superior occipital gyrus			L	-16	-92	2	4.28
Putamen	169	.037	L	-28	-14	0	4.39