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Empathic Competences during Social Interactions in Autism Spectrum Disorder – an fMRI Study.

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"Empathy is about finding echoes of another person in yourself."

– Moshin Hamid[1]

[1] Source: Leyshon, C. (2012, September 16). This Week in Fiction: Moshin Hamid. *The New Yorker*. Retrieved from: http://www.newyorker.com/books/page-turner/this-week-in-fiction-mohsin-hamid (last access 2017-05-14)

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Contents

1 Theoretical Background

Philosophers and scientists have long since pondered the question which qualities make human cognition so unique among animals, even when comparing us to our closest primate relatives. Looking at this problem from a psychological perspective, it is not hard to arrive at the conclusion that one defining characteristic seems to be the fact that humans are particularly adept at complex social functioning and that this has given us distinct evolutionary advantages (Pinker, 2010). In other words, humans are exceedingly proficient in "social cognition", a term which covers a variety of mental processes involved in the understanding and storing of information about ourselves and other people, as well as knowledge about social norms and procedures that allow us to successfully conduct interpersonal relationships and maneuver in the social world (Van Overwalle, 2009). As humans, our advanced social cognitive abilities allow us to navigate all kinds of complex social situations. We are able to recognize and think about the somatic and mental states both of ourselves and others and make deductions about their goals and motivations. Consequently, we benefit from these abilities by letting this knowledge guide our interactions with others by engaging in complex collaborative activities, a defining feature of our species (Amodio & Frith, 2006; Gallese, 2006; Heberlein & Adolphs, 2005; Tomasello, Carpenter, Call, Behne, & Moll, 2005). Or, as Tomasello and colleagues put it, „Human beings are the world's experts at mind reading" (Tomasello et al., 2005, p. 28).

Recently, the field of social cognitive neuroscience has begun to discover the underlying neural substrates of some of the basic processes that are involved in many aspects of social cognition (Amodio & Frith, 2006; Heberlein & Adolphs, 2005) by combining theories from social and developmental psychology with modern neuroimaging techniques such as electroencephalography (EEG), functional magnetic resonance imaging (fMRI) or repetitive transcranial magnetic stimulation (rTMS), giving us insight into what might be happening on a biological level when we interact with others, share their feelings or try to mentally represent their beliefs (Singer, 2006). However, the range of socio-cognitive abilities is broad and social cognition is a vast and complicated topic consisting of a multitude of different processes. It is therefore first necessary to precisely define the construct one wishes to investigate to be able to pinpoint the exact neural circuitry underlying said process.

1.1 Empathy and Related Concepts

The concept of empathy is a key aspect of social cognition and an important and widely researched phenomenon in social cognitive neuroscience (Bird et al., 2010; Zaki & Ochsner, 2012). Even though - or possibly because - there is so much research in this area, there is still a lack of consensus on the exact definition of empathy and how it interconnects with related concepts. In everyday life, empathy is a complicated and multifaceted construct that includes many neurocognitive mechanisms and the lay term "empathy" is often used interchangeably with other socio-cognitive concepts such as compassion, sympathy, Theory of Mind, or prosocial behavior. However, while these processes are certainly related to empathy and often take place in similar contexts, there are some significant differences (de Vignemont & Singer, 2006; Preston & de Waal, 2002).

The term *empathy* comes from the German word *Einfühlung* (literally "feeling into") and was mainly used in the psychology of aesthetics before it was translated into English by psychologist Edward Titchener in 1909 (Eisenberg & Strayer, 1990). Today, empathy generally refers to "the ability to vicariously experience and to understand the affect of other people" (Lockwood, 2016) or, in other words, to feel and understand what another person is feeling. De Vignemont and Singer (2006) give a more detailed definition and characterize four conditions that must be met for empathy to occur: Firstly, a person must be in an affective state. Secondly, said affective state must be the result observing or imagining the affective state of another person, and, thirdly, it must be isomorphic to (i.e. the same as) the other person's affective state. Lastly, the perceiver must know that his or her own feelings were elicited by the other person's affective state (i.e. the other person's feelings are the source of their own feelings). Following this definition, we can now attempt to distinguish empathy from other socio-cognitive concepts all which do not meet one or more of the conditions set by de Vignemont and Singer (2006). The most important of these and how they relate to the empathy criteria can be seen in Table 1.

Emotional contagion is thought of as a sub-class of empathy. It can often be observed in young children (e.g. when a baby starts crying simply because another one does) and is theorized to help benefit the early mother-infant bond (Lockwood, 2016; Preston & de Waal, 2002). While it describes an affective state isomorphic to another persons', there is a lack of *self-other distinction*, that is, the person is not aware of the source of the affective state and cannot distinguish between their own feelings and those of another individual (Bird & Viding, 2014; Lockwood, 2016). Emotional contagion is therefore a necessary but insufficient precursor to empathy, since the forth criterion of the definition above is not met. Similarly, *emotional imitation* or *mimicry* is the automatic and involuntary synchronization of emotional behavior, a process which involves the imitation of emotional expressions (whether they are vocal, facial or postural) of another individual (Bird & Viding, 2014; Walter, 2012). Like empathy, imitation relies on shared representations between the self and other, and it has been hypothesized that (internally) copying another's expressions can lead to empathy ("motor theory of empathy"; Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Leslie, Johnson-Frey, & Grafton, 2004). However, not all scholars agree that imitation is a necessary prerequisite for empathy (de Vignemont & Singer, 2006). *Sympathy*, on the other hand (also referred to as *compassion* or *empathic concern*), does not involve a vicarious experience, that is, there is no isomorphic emotional state between the observer and the object of their sympathy (Walter, 2012). Sympathy is generally considered an affective state related to another individual's negative emotional experience (e.g. I might feel pity when I see another person who is sad, but might not feel sad myself) and may lead to *prosocial behavior* in order to reduce that person's suffering. As such, compassion is inherently other-oriented, which is not necessarily the case for empathy (Bird & Viding, 2014; Lockwood, 2016; Singer & Klimecki, 2014). Additionally, Walter (2012) describes *personal distress*, a negative affective state that is also caused by another's emotional state, but is self-oriented rather than other-oriented, as opposed to sympathy (e.g. personal distress at the sight of someone's suffering might cause me to turn away to make myself feel better). Another process closely related to empathy is *mentalizing* or *Theory of Mind* (ToM). It broadly refers to the cognitive ability to represent another individual's mental states, such as beliefs, desires and intentions, but also emotional states. The attribution of mental states to ourselves and others allows us to explain someone's behavior and even predict their future actions (C. Frith & Frith, 2005; Goldman, 2012). Mentalizing is a form of *metacognition*, which describes the ability think about one's own and other's thoughts, and it can reach several levels of complexity. For example, while first-order ToM involves thinking about someone else's beliefs, second-order ToM describes thinking about others' metacognition (e.g. I know, that you know, that I know something). Because ToM is a cognitive process, it is not necessary that the subject himself is in an affective state, but the ability to infer another's feelings is seen as an essential part of empathy and is sometimes considered a form of empathy on its own (Blair, 2005). Lastly, *perspective taking*, the ability to assume the mental perspective of another (or "putting oneself in someone's shoes"), is a mechanism linked to ToM and is a requirement for explicit self-other distinction and therefore empathy (Walter, 2012).

Table 1

Socio-cognitive concepts in relation to empathy criteria.

Socio-cognitive concept	Affective experience	Elicited by another Person	Isomorphic State	Self-other distinction
Emotional Contagion	x	x	x	
Emotional Imitation		x		
Sympathy	x	x		x
Theory of Mind				x
True empathy	x	x	x	x

Note. Adapted from "Social Cognitive Neuroscience of Empathy – Concepts, Circuits and Genes" by H. Walter, 2012, *Neuroscience, 4(1)*, 9–17.

1.2 Neurocognitive Theories on Empathy

Evidence from neuroimaging studies suggests that the above mentioned concepts are closely related and most likely all part of a greater socio-cognitive structure with specific but overlapping neural systems that cannot be completely separated from each other (Preston & de Waal, 2002). For example, representing others' mental states (i.e. Theory of Mind) is associated with activations in the temporoparietal junction (TPJ), the medial prefrontal cortex (mPFC), and the temporal poles (U. Frith & Frith, 2003; Lamm, Decety, & Singer, 2011). Emotional imitation, on the other hand, is closely linked to mirror neuron systems and correlated with activity in the inferior frontal gyrus (IFG) and the inferior parietal cortex (IPC; Bird & Viding, 2014; Catmur, Walsh, & Heyes, 2009). Most of these brain areas have also been associated with various empathy tasks, which corroborates the idea of a greater empathy network (Lockwood, 2016; Singer & Lamm, 2009).

One generally accepted concept underlying most contemporary theories of empathy is that of shared neural networks: When we share the emotions of another person (or internally represent their mental state), it triggers certain neural structures, some of which are also active when we ourselves experience that emotion or mental state (Singer & Lamm, 2009). This was first discovered for motor actions (observing intentional hand movements of another person activates the same motor neurons as performing that action oneself) and it was suggested that this process forms the foundation of understanding another's intentions (Gallese, 2006). The associated neurons were aptly named "mirror neurons" and the same basic mechanism was soon observed for, among others, emotional facial expressions (Wicker et al., 2003), touch (Keysers et al., 2004), and pain (Singer et al., 2004). It is important to note, however, that the self-related and other-related neural activations never completely overlap. For example, Singer et al. (2004) were able to show that being exposed to a painful stimulus and seeing another receive a painful stimulus both activated the anterior cingulate cortex (ACC), the anterior insula (AI), the brainstem and the cerebellum. However, only receiving pain directly activated the secondary somatosensory cortex, the sensorimotor cortex and the caudal ACC. This suggests a clear differentiation between feeling empathy for pain and feeling pain oneself.

Based on this theory of shared neural networks, and arguing that there has been an overemphasis on differentiating between empathy and related socio-cognitive phenomena, Preston and de Waal (2002) introduced their Perception-Action Model of empathy, integrating the various processes into one broadly defined construct of empathy by combining data from behavioral as well as physiological and functional neuroanatomical research. They propose that observing or imagining another individual's affective state automatically leads to a representation of that affective state in the observer, which is accompanied by corresponding autonomic and somatic reactions. Per this model, processes like emotional contagion, mentalizing or sympathy all function under this mechanism and can be subsumed under one super-category of empathy. The authors' emphasis on the automatic activation of empathy without conscious effort highlights the importance of basic processes such as mimicry and is supported by several studies and fits nicely with the theory of shared neural networks (Singer & Lamm, 2009). However, while a reproduction of sensorimotor, affective or mental states through shared neural representations is certainly essential for socio-cognitive processes, the Perception-Action model focusses heavily on the idea that empathy is activated automatically without conscious effort, that is, in a bottom-up process. Nonetheless, the prevailing view in recent models is that top-down control and contextual appraisal are just as important and are involved in either creating the empathic response or at least regulating it (Singer & Lamm, 2009). After all, in our everyday lives, we are constantly confronted with other people's emotions through facial cues, body language or more explicit forms of communication, but we do not find ourselves in a constant state of empathy. Therefore, there must be some regulatory mechanisms that help us cope with other people's emotions and modulate our experience of empathy.

Decety and Lamm (2006) suggest a model of empathy that integrates both bottom-up information processing related to the automatic sharing of emotions (analogous to the above mentioned Perception-Action model), as well top-down information processing involving voluntary control, responsible for moderating the experience through the use of executive function resources. These cognitive strategies can be employed to either down-regulate (i.e. reduce) or up-regulate (i.e. increase) the own emotional response. It is arguable that downregulation would be used more often in everyday empathic situations, most likely avoid emotional overstimulation or personal distress. For example, it would not be useful to have an excessive emotional response to seeing people in distressing situations which we have no control over (e.g. tragic events on the news), but we also need to down-regulate our own emotional responses if we want to effectively help other in a negative emotional state (e.g. soothing a crying baby). However, the authors argue that up-regulation could also play an important role, for example when we want to increase our compassionate response to people with whom we usually do not emphasize (e.g. out-group members). In either case, top-down cognitive control allows us to select appropriate reactions to a situation and curb inappropriate ones using various strategies such as attentional control (e.g. placing selective focus on specific sensory inputs) or cognitive change (e.g. re-evaluating affective information). A number of neuroscientific studies have found substantiating evidence for this theory (see Singer & Lamm, 2009, for a review). For example, in one fMRI study participants were confronted with pictures of painful situations. When they had to rate the intensity of pain felt by the person in the picture, participants showed increased activation in areas that are also associated with first-hand experience of pain, namely the anterior cingulate cortex (ACC) and the right middle frontal gyrus (MFG) compared to when they looked at neutral stimuli. However, when participants were made to reorient their attention (by asking them to count the number of hands visible in the pictures), no activation in the insular or cingulate cortex was found (Gu & Han, 2007). Similar results were reported for the role of contextual appraisal (Lamm, Nusbaum, Meltzoff, & Decety, 2007): Participants were shown pictures of hands receiving seemingly painful needle injections, which correlated with activation in the anterior insula (AI) and the medial cingulate cortex (MCC), both components of the pain matrix. When participants were informed that these injections were in fact not painful because anesthesia had been applied beforehand, the activation was still there (which suggests an automatic response to such salient stimuli), but they also showed increased activity in the temporoparietal junction and the orbitofrontal cortex, regions associated with self-other distinction and valence attribution, which reinforces the idea that cognitive reappraisal was taking place. In summary, it seems evident that both bottom-up and top-down processes are equally important contributors to the formation of empathy.

In fact, many authors have recently moved towards defining empathy as consisting of two essential elements which rely on separate neural networks: an affective and a cognitive component (Batson, 2009; Eres, Decety, Louis, & Molenberghs, 2015; Krämer, Mohammadi, Doñamayor, Samii, & Münte, 2010; Shamay-Tsoory, Aharon-Peretz, & Perry, 2009). In that context, *affective empathy* refers to the bottom-up regulated automatic tendency to share others' emotional states and is related to processes such as emotional contagion and imitation. It is associated with activation in the same limbic regions that are active during affective experiences (Masten & Colich, 2011). On the other hand, *cognitive empathy* refers to the ability to perceive and correctly identify others' affective states. It is essentially a form of Theory of Mind (Blair, 2005) and relies on the correlated neural networks such as the ventromedial, medial and dorsomedial prefrontal cortex (PFC), the posterior superior temporal sulcus (pSTS), the temporal poles, the posterior cingulate cortex (PCC) and the precuneus (Amodio & Frith, 2006; de Vignemont & Singer, 2006; Masten & Colich, 2011). Smith (2009) argues that individuals can differ in their propensity for either component, and that this can lead to different kinds of empathy disorders. Nevertheless, both cognitive and affective empathy are essential components for experiencing true empathy, and the processes cannot be completely separated from each other (Walter, 2012).

1.3 Empathy for Pain and Social Exclusion

While social neuroscience has studied humans' empathic reactions in relation to a number of emotions (e.g. disgust, anxiety, or anger) and sensations (e.g. taste or touch), the largest part of neuroimaging studies has focused on empathy for pain (Bernhardt & Singer, 2012; de Vignemont & Singer, 2006). In general, negative emotions elicit stronger affective reactions, and because pain is a highly salient aversive sensation, it will reliably produce a response in an observer, which makes it an ideal stimulus for empathy studies (Bernhardt & Singer, 2012; Preston & Hofelich, 2012). As mentioned above, numerous studies have found that areas activated during empathy for pain show a significant overlap with first-hand experience of pain. Various researchers replicated the results of the early influential study by Singer et al. (2004) which found activations in the anterior insula (AI), anterior cingulate cortex (ACC), brainstem, and cerebellum for both first- and second-hand experience of pain (see section 2.2). For example, an fMRI study by Jackson, Meltzoff, and Decety (2005) presented participants with pictures of hands and feet in painful situations. Assessing the level of pain was associated with changes in activation in the ACC, the AI, the cerebellum and the thalamus; with the activity in the ACC correlating strongly with rating another's pain. Lamm et al. (2011) conducted a meta-analysis on studies concerning empathy for pain and also found consistent evidence for involvement of the AI and the medial ACC. Additionally, activation occurred in areas related to inferring and representing mental states (i.e. Theory of Mind), namely the precuneus, the ventromedial prefrontal cortex (vmPFC), the superior temporal cortex (STC) and the temporoparietal junction (TPJ). These results paint a consistent picture about the neural underpinnings of empathy for pain and once again support the hypothesis that there are significant overlaps between networks that are activated during vicarious as well as direct experience of emotions. However, while empathy is a social emotion, pain in and of itself is not. To garner more ecologically relevant insights into the workings of social cognition in everyday human interactions, some researchers have therefore turned towards investigating empathy for social pain, which is most often elicited through paradigms of social exclusion or ostracism. *Ostracism* can be described as being ignored or excluded from social activities and often happens without explanation (Williams, 2007). Social pain is remarkably similar to physical pain, a fact which is reflected not only in our language (e.g. someone can "hurt our feelings") but also in our neural networks: social exclusion elicits large parts of the same networks as physical pain (Eisenberger, Lieberman, & Williams, 2003) As inherently social creatures, we are driven to seek out the presence of others and if we are rejected or left behind by them, it can cause severe distress and impact our self-esteem and sense of control (Eisenberger et al., 2003; Seidel et al., 2013). From an evolutionary perspective, ostracism presents a threat to our wellbeing (Williams, 2007), especially if we are very young and still dependent on our caregivers. It is therefore logical that the social attachment system is closely linked to the pain system, and that separation triggers an aversive, painful response as a survival mechanism (Nelson & Panksepp, 1998). Pain (both social and physical) has the function of informing us that something is amiss, and several studies have found that the ACC will act as a sort of "alarm system" in this context (Eisenberger et al., 2003).

To test the effects of ostracism empirically, Williams, Cheung, and Choi (2000) developed a virtual game called "Cyberball", in which participants believed they were playing an interactive ball-tossing game with two other players, represented by comic avatars connected via the internet. Goal of the game was to catch and throw a virtual ball around. In reality, there were no other players as the game was pre-determined, and after a while the participants were deliberately excluded, as the other "players" stopped passing them the ball. Even though this was a rather artificial situation with no actual social contact, the authors could induce feelings of social pain. The longer participants were excluded from the game, the more negatively they rated their mood. Several other studies were able to reproduce these effects using the Cyberball paradigm (Abrams, Weick, Thomas, Colbe, & Franklin, 2011; Kawamoto, Nittono, & Ura, 2013; Seidel et al., 2013; van Noordt, White, Wu, Mayes, & Crowley, 2015).

Using the same game, Eisenberger et al. (2003) conducted an fMRI study and found activation of the ACC during exclusion, which correlated positively with self-reported distress. Additionally, the authors found activation in the right ventral prefrontal cortex (rvPFC), which correlated negatively with distress and modulated changes in the AC. These results suggest that the rvPFC disrupts activity in the ACC to regulate feelings of distress during social exclusion. While the studies mentioned so far focused on social pain per se and not empathy, other researchers were able to show that empathy for social pain activates the AI, ACC and MCC, similar neural networks as empathy for physical pain (Bernhardt & Singer, 2012). Masten, Morelli, and Eisenberger (2011) let participants in an fMRI scanner observe a person being excluded by two others. Observing exclusion was associated with activation in the dorsomedial and medial PFC as well as the precuneus (regions associated with mentalizing). Very empathic individuals additionally activated the AI and dorsal ACC, regions associated with social pain. This activation was also correlated with subsequent prosocial behavior toward the "victim". In another fMRI study, Novembre, Zanon, and Silani (2015) used a modified and updated version of the Cyberball paradigm to induce empathy for social exclusion and compared this with an empathy-for-pain task. They found that first-hand and second-hand experience of social pain resulted in activations of the same somatosensory regions as physical pain, namely the posterior insula (pINS) and the secondary somatosensory cortex (SII). Furthermore, they found only one region that was active for both types of empathy: the subgenual cingulate cortex. However, they were not able to replicate findings from previous studies, which implicated activations in the AI, pACC and aMCC during social exclusion. To summarize, the findings reported above show that social pain is a strong stimulus that reliably produces a robust empathic response. However, empathy is not a perfect mechanism and in fact, studies indicate humans seem consistently to make errors when judging others' emotional states.

1.4 Emotional Egocentricity Bias and Altercentric Bias

Because we cannot literally take another person's place or their perspective, we are forced to always use our own experiences and feelings as a basis when we try to judge someone else's affective state (Bird & Viding, 2014). This is substantiated by the neuroscientific evidence of overlapping neural systems during first-hand and second-hand emotional experiences (Preston & de Waal, 2002): to feel empathy for a person in a particular emotional state, we activate brain regions that are responsible for feeling that emotional state.

However, at the same time, empathy would not be possible without self-other distinction. While emotional contagion would probably take place, we would have no way of identifying the source of our feelings (Bird & Viding, 2014; Lockwood, 2016). When self-other distinction fails, the self-referential mechanism takes over and we project our own mental state onto the other person, which can lead to incorrect judgments of other's affective states (e.g. I am happy, so I assume my friend is too, even though she is sad). This is called *Emotional Egocentricity Bias*, or *EEB* (Lamm, Bukowski, & Silani, 2016). While a cognitive egocentricity bias has been well documented (Epley, Keysar, van Boven, & Gilovich, 2004; Royzman, Cassidy, & Baron, 2003), there have been only few studies researching this intriguing phenomenon in the emotional domain. Silani, Lamm, Ruff, and Singer (2013) created a special visuo-tactile paradigm specifically to measure the EEB. They elicited pleasant or unpleasant feelings in participants by touching their hands with positive or negative stimuli (e.g. something soft or something slimy). While the participants' hands were not visible to them, they were shown a picture that corresponded to the pleasant or unpleasant feeling they were experiencing (e.g. a rose petal or a snail). At the same time, they were also shown a picture of what another participant, who was in the room with them and undergoing the same experiment, was currently being touched with. Participants were then asked to put themselves in the position of the other person and rate the feelings that person was currently experiencing on a scale from negative to positive. Sometimes, the participants and the other person were in an incongruent state (i.e. one was feeling pleasant touch while the other was feeling unpleasant touch) and other times they were in a congruent state (i.e. both feeling pleasant or unpleasant touch). The authors showed that there was a difference in how participants rated the other person's feelings depending on whether they were in a congruent or incongruent state. In the incongruent trials, the ratings were consistently biased in the direction of the participants' own feeling states, compared to congruent trials (e.g. when the other person was feeling unpleasant touch but the participant was feelings pleasant touch, they rated the other person's feelings as less negative then when they themselves were feeling unpleasant touch as well). This indicates that participants used their own emotional state as a guide for judging the other person's state. It became apparent that in incongruent situations, participants had trouble with self-other distinction and thus made inappropriate emotionally biased judgements. In a follow-up fMRI experiment, Silani et al. (2013) found activation of the right supramarginal gyrus (rSMG) during judgment of the other person, but not during self-judgment; as well as an increased interaction of the rSMG with the primary and secondary somatosensory cortex (SI and SII), which could indicate that some mechanism to overcome the bias was taking place. Interestingly, the rSMG is clearly anterior to the rTPJ, an area that previous studies had consistently found for such tasks (Decety & Lamm, 2007). In a final experiment, Silani et al. (2013) used transcranial magnetic stimulation to temporarily disrupt the rSMG while participants were performing the empathy task. This lead to a substantial increase in the EEB, which suggests that the rSMG is an area involved in overcoming the EEB.

Using a slightly different paradigm to investigate the EEB, Steinbeis, Bernhardt and Singer (2014) found that children had a higher EEB than adults, which correlated with reduced activity in the rSMG as well as lower connectivity with the left dorsolateral prefrontal cortex (DLPFC). Tomova, Von Dawans, Heinrichs, Silani and Lamm (2014) on the other hand found that stress can influence self-other distinction: while women showed higher self-other distinction in stressful situations, men displayed an increased egocentricity bias, which suggests that for them, acute stress led to a higher cognitive load which in turn led to a reduced capacity to distinguish between the self and other. To summarize, the existence of the EEB has been shown in several experiments, and it has been reliably connected with the rTPJ and the rSMG, the latter of which is most likely involved in overcoming the bias and restoring self-other distinction. While healthy adults are usually quite adept at judging others' emotional states, some level of bias still exists, and it is influenced by situational components such as stress (Lamm et al., 2016).

However, what happens if the task is not to infer someone else's emotional state, but to correctly assess our own feelings? Some research suggests that there might be a converse mechanism to the EEB, called the *Altercentric* or *Allocentric Bias* (AB), which describes the tendency to be influenced by others' affective state when we are asked to rate our own, in a process like emotional contagion. Though not strictly empathy, it is still an interesting phenomenon to explore in this context, since the underlying mechanism leading to both the EEB and the AB may be the same, namely a malfunction in self-other distinction. So far, there has been some research on the Altercentric Bias concerning tasks in the cognitive domain, such as automatic perspective taking (Capozzi, Cavallo, Furlanetto, & Becchio, 2014; Samson, Apperly, Braithwaite, Andrews, & Scott, 2010; Surtees & Apperly, 2012), but almost no studies have investigated the Altercentric Bias in the emotional domain. Hoffmann et al., (2016a) used the visuo-tactile paradigm developed by Silani et al. (2013) to investigate deficits of self-other distinction in depression by measuring both the EEB and the AB. They found that in congruent conditions (i.e. when self and other were in the same affective state) depression did not influence empathic judgements. In incongruent trials, on the other hand, subjects with major depressive disorder (MDD) showed increases in both the EEB and the AB. The heightened Altercentric Bias speaks for an increase in emotional contagion, which is in line with studies on empathy in depression that suggest that MDD patients often show greater levels of personal distress (Schreiter, Pijnenborg, & Aan Het Rot, 2013). This in turn suggests a defect in self-other distinction, as it would normally act in a regulatory capacity (Decety & Lamm, 2006). Directly comparing the EBB and the AB in a neuroimaging study could provide further knowledge about the exact mechanism of empathy. Even given the great amount of research on the strength of the egocentric perspective both in the cognitive and affective domains, it seems like the bias towards one's own feelings would possibly a stronger force than the opposite (i.e. the AB).

1.5 Empathic Competences in Autism Spectrum Disorder

Aside from depression, there are several clinical conditions (sometimes referred to as *empathy disorders*) which are associated with a deficit in empathic competence/skills, including autism, sociopathy, frontotemporal dementia, damage to the prefrontal cortex, anorexia nervosa and even certain personality disorders (Decety & Jackson, 2004; Hoffmann et al., 2016a; Preston & de Waal, 2002). However, these clinical populations differ greatly in how they are affected by empathy or a lack thereof (Blair, 2005; Smith, 2009) and studying them can provide essential insights into the neural structures underlying social cognition and help build a more comprehensive model of empathy.

The term *Autism Spectrum Disorder* (ASD) describes what was formerly thought of as a group of closely related disorders (including autistic disorder and Asperger's syndrome) that share common pathophysiological mechanisms, specifically deficits in social communication and a restricted set of behaviors and interests (Durand, 2014; Frith & Happé, 2005). The fifth edition of the Diagnostic and Statistical Manual of Mental Disorders (DSM-5) eliminated the differentiation of individual conditions and created one comprehensive disorder with two main diagnostic criteria: individuals with ASD will exhibit, firstly, "persistent deficits in social communication and social interaction across multiple contexts" and secondly, "restricted, repetitive patterns of behavior, interests or activities" (American Psychiatric Association, 2013, p. 50). These characteristics can manifest themselves as a range of symptoms such as: inadequate understanding of social cues and nonverbal communication, reduced sharing of interests and emotions with others, problems in maintaining interpersonal relationships, difficulties adjusting behavior to varying social contexts, as well as stereotyped motor movements or speech patterns, intense but restricted areas of interest, or uncompromising adherence to rituals or routines, among many others (American Psychiatric Association, 2013; Frith & Happé, 2005). It is important to note, however, that the term "spectrum disorder" signifies the great heterogeneity of symptom severity in this disorder, and impairments can range from individuals needing only some support and being able to lead regular everyday lives to severe cases requiring very substantial support (Durand, 2014). *Asperger's Syndrome* (AS) is a subcategory of autism that was used as a diagnosis until 2013 but has been eliminated in the DSM-5. While it is characterized by the typical symptoms described above, these are not accompanied by the developmental delay in language or cognitive abilities that can be seen in more severe cases of autism (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001; Volkmar & McPartland, 2014).[2]

Autism Spectrum Disorder has been studied extensively in conjunction with research on empathy and social cognition, and for a long time the prevailing theory was that people with ASD show a general lack of empathy (Blacher, Kraemer, & Schalow, 2003; Preston & de Waal, 2002; Shamay-Tsoory, Tomer, Yaniv, & Aharon-Peretz, 2002). For example, as Baron-Cohen (2009) explains in his introduction to the Empathizing-Systemizing (E-S) Theory of autism, subjects with ASD generally score high on the Systemizing Quotient (a factor describing the impulse to analyze or construct systems), but receive low scores on the Empathizing Quotient (a construct measuring both cognitive and affective aspects of empathy). A similar result was found by Johnson, Filliter, and Murphy (2009) who compared both self-report and parent-report data of children with ASD via the systemizing and empathizing quotients. Furthermore, autistic individuals tend to have lower scores on self-report report measures of empathy such as the interpersonal reactivity index (IRI; Davis, 1983) or the empathy quotient (EQ; Baron-Cohen & Wheelwright, 2004; Lombardo, Barnes, Wheelwright, & Baron-Cohen, 2007). On a physiological level, Minio-Paluello, Baron-Cohen, Avenanti, Walsh and Aglioti (2009) found that people with ASD, as opposed to healthy control participants, did not show a correlated neurophysiological response when faced with video clips of other people in pain, which speaks for a lack of empathy embodiment.

However, other recent research shows that the poor performance of subjects with ASD on certain empathy tasks may be due to disruptions in specific components of empathy rather than a general empathy deficit (see Baird, Scheffer, & Wilson, 2011 and Frith & Happé, 2005, for reviews). For example, Rogers, Dziobek, Hassenstab, Wolf and Convit (2007) administered the IRI and a ToM measure (the strange stories test; Happé, 1994) to 21 adults with Asperger's

[2] Because methodological and ethical constraints of the experiment described in this thesis necessitated the participation of people with at least an average level of intelligence, the autistic subjects invited to participate in this study all carried a diagnosis of Asperger's syndrome.

syndrome and a matched control group. They found that participants with ASD achieved lower scores on cognitive empathy and Theory of Mind, but they did not differ from neurotypical controls on the empathic concern scale and even had higher scores on the personal distress scale (both being part of the affective empathy scale of the IRI). These results were later replicated with a more naturalistic empathy measure, the multifaceted empathy test (MET; (Dziobek et al., 2008). These findings are in line with established evidence suggesting that a deficit in Theory of Mind is one of the core criteria of ASD (Baron-Cohen, Leslie, & Frith, 1985; Happé, 1994; Hill & Frith, 2003; Senju, Southgate, White, & Frith, 2009), a characteristic which has often been described as “mind-blindness” (Smith, 2009). The idea that there is a dissociation between cognitive and affective empathy in ASD was also taken up by Smith (2009) in his “Empathy Imbalance Hypothesis of Autism”. He postulates that while people with ASD do indeed exhibit lower levels of cognitive empathy, they may even have an excess of affective (or emotional) empathy; and that autistic people develop a distinct cognitive-behavioral style early in life to cope with this imbalance, which in turn explains many of the symptoms of autism.

Recently, several studies have also used neuroimaging techniques to investigate the relationship between Autism Spectrum Disorder and empathy. For example, McPartland et al. (2011) used the Cyberball paradigm to induce feelings of social exclusion conducted an EEG study with children with ASD and a group of typically developing children. They found that while both groups reported the same amount of personal distress, there was a difference in the temporal processing of rejection events, suggesting that children with ASD had reduced attentional processes during the negative social situation. Similarly, Bird, Catmur, Silani, Frith, and Frith (2006) found that people with ASD showed a lack of attentional modulation when they were presented with a social stimulus. On a neurological level, this was associated with a decrease in connectivity modulation between the primary visual cortex (V1) and the extrastriate areas (responsible for attention). Lombardo et al. (2009) found evidence for reduced SOD in autism. Neurotypical control participants showed more activation in middle cingulate cortex (MCC) and the ventromedial prefrontal cortex (vmPFC) during self-related mentalizing (as compared to other-related mentalizing). However, people with ASD recruited the vmPFC for both tasks, while the MCC was more active during other-related processing. On the other hand, Philip et al., (2012) reported that participants with ASD showed changes in activation in the superior temporal gyri (STG) as well as the superior temporal sulci (STS) during mentalizing tasks. Additionally, they found increased activation in the right inferior frontal gyrus (IFG) and a decrease in activation in the left inferior parietal lobule (IPL), which are both associated with the human mirror neuron system and perspective taking. However, the authors could not report changes in activity in the ACC, as previous studies had (Philip et al., 2012). Finally, Hoffmann, Köhne, Steinbeis, Dziobek, and Singer (2016b) used an affective touch paradigm to investigate competences in self-other distinction in participants with ASD and neurotypical controls. While the EEB was of similar size for both groups, only people with ASD also showed a deficit in ToM. The authors also found that the right SMG was connected to areas relevant to emotion processing, while the right TPJ showed connections to the mPFC, the PC and the PCC, areas involved in Theory of Mind and cognitive empathy. This network showed reduced resting state connectivity for people with ASD. Finally, in addition to the research on deficits of cognitive empathy in ASD, there is some evidence that a comorbidity with alexithymia may also have a significant impact on empathic skills. *Alexithymia* is a subclinical condition characterized by the inability to identify and describe emotions (Lamm et al., 2016). While alexithymia occurs in the natural population with a prevalence of about 10%, evidence shows that this percentage is much higher in people with ASD, namely around 50% (Bird et al., 2010; Silani et al., 2008) and some recent studies suggest that some of the deficits in socioemotional processing typically associated with ASD may in fact be due to this comorbidity (Lamm et al., 2016).

To summarize, the current state of knowledge on empathy and autism suggests that people with ASD can indeed have vicarious emotional experiences, and that poor performance or low scores on an empathy task or questionnaire is most likely not due to overall lack of empathy, but a deficit in the cognitive component of empathy, specifically self-other distinction. This can present itself in an increased Emotional Egocentricity Bias and possibly also an increased Altercentric Bias. Although this has not yet been studied, there is some evidence that people with ASD might sometimes adopt an extreme version of altercentrism (see Frith & De Vignemont, 2005). Finally, a comorbidity with Alexithymia may also have a significant influence on empathy skills in autism.

1.6 Limitations of Past Research

Empathy and related social-cognitive concepts have certainly been subject to a substantial number of experiments and theories, yet there are still some unanswered questions. Although there has been a significant amount of research on empathy for pain, the exact mechanisms of empathy for social pain and social exclusion are still unclear (Preston & de Waal, 2002). Investigating the pathologies of empathy (such as in Autism Spectrum Disorder) can help to clarify this issue by linking specific empathy deficits to underlying neural processes.

While various studies have indeed explored the relationship between ASD and socio-cognitive skills, most of them focused on the development of mentalizing skills and thus mainly studied children or adolescents (C. Sebastian, Blakemore, & Charman, 2009; Singer, 2006). It would therefore be interesting to look at higher-order empathic competences in adults with ASD using a task that mimics genuine social interactions in a relatively naturalistic way, in order to be able to make more generalized statements about empathy in ASD.

Additionally, even though egocentricity in the cognitive domain has been well documented (Epley, Keysar, van Boven, & Gilovich, 2004; Royzman, Cassidy, & Baron, 2003), the same is not the case for the affective domain, and the concept of an Emotional Egocentricity Bias is relatively new (Silani et al., 2013). Even less research has been done regarding the Altercentric Bias, although there is some evidence that suggests that its closely related to the EEB and SOD: not only does a lack of self-other distinction seem to impact empathic competences during the judgement of another's affective state (in the form of an EEB), but also may lead to inaccurate judgements of one's own emotional state through emotional contagion (i.e. the AB; Hoffmann et al., 2016a). While much research has been conducted on empathy in autism through a variety of paradigms and employing a variety of methods (for examples, see Bird et al., 2010; Minio-Paluello et al., 2009; Rogers et al., 2007; Schulte-Rüther et al., 2011; Shamay-Tsoory et al., 2002), so far, only one study has investigated self-other distinction in ASD (Hoffmann et al., 2016b), and none have explored its relationship to empathic skills in situations of ostracism. Finally, although one study investigated and compared the AB and the EEB in individuals with depression (Hoffmann et al., 2016a), the two have not been directly compared in an autistic sample.

2 Research Goal and Hypotheses

This fMRI study aims to increase scientific knowledge about the phenomena of empathy, self-other distinction, and emotional contagion by comparing adults with ASD with a control group from the neurotypical population. Feelings of social pain will be established using a modified version of the Cyberball paradigm developed by Novembre et al. (2015), which allows the creation of congruent and incongruent affective states through exclusion and inclusion in a virtual social situation. These can then be compared for both the judgement of the participants' own as well as another's emotions to establish existence of the AB and EEB. The combination of behavioral and neurophysiological data will shed light on the neural underpinnings of empathy in general and self-other distinction and emotional contagion in particular. This thesis contains two studies. Study 1 will investigate the existence of the EEB and the AB in the general population, by putting a sample of healthy adults in situations of social inclusion and exclusion and asking them to alternatively rate their own affective state or that of another person. In Study 2, a group of participants with ASD will undergo the same experimental paradigm and will be compared to a group of matched neurotypical controls. This should allow for a direct comparison of the EEB and the AB between the two groups. Though previous studies have showed mixed results on deficits in self-other distinction with regards to ASD (Hoffmann et al., 2016b), most researchers agree that SOD is impaired in autism (Lamm et al., 2016) and so it is expected that subjects with ASD will show a higher EEB as well as a higher AB in this experiment. Finally, it is expected that that the neuroimaging data will show activations in brain regions associated with empathy and self-other distinction. The hypotheses follow as such:

2.1 Hypotheses Study 1

H1: During the empathic judgement of the opposite person, there will be an Emotional Egocentricity Bias, presenting itself in a difference in ratings between the congruent and incongruent conditions, accompanied by an increase in activation of the neural networks associated with self-other distinction, namely the right temporoparietal junction (rTPJ) and the right supramarginal gyrus (rSMG).

> **H1.1:** Inclusion Bias: When the other person is excluded, the average rating will be lower (i.e. more negative) when the rater themselves is also excluded (congruent condition) than when the rater is being included (incongruent condition).

H1.2: Exclusion bias: When the other person is included, the average rating should be higher (i.e. more positive) when the rater themselves is also included (congruent condition) than when the rater is being excluded (incongruent condition).

H2: During the judgement of the self, there will be an Altercentric Bias (emotional contagion), resulting in a difference in ratings between the congruent and incongruent trials, accompanied by an increase in activation of the neural networks associated with self-other distinction, namely the (rTPJ, rSMG).

H2.1: When the self is excluded, the average rating of the self should be lower (i.e. more negative) when the opposite person is also excluded (congruent condition) than when the rater is being included (incongruent).

H2.2: When the self is included, the average rating should be higher (i.e. more positive) when the opposite person also included (congruent condition) than when they are being excluded (incongruent).

H3: When comparing the two biases, there should be a difference in size between the EEB and the AB, with the EEB being larger than the AB.

2.2 Hypotheses Study 2

H4: When compared to neurotypical controls, participants with ASD will demonstrate a deficit in self-other distinction, which will present itself in a larger bias during judgments of emotional situations. This will be accompanied by a decrease in hemodynamic activity in the regions associated with SOD (rTPJ, rSMG).

H4.1: During empathic judgments of the opposite person, ASD participants will show a higher EEB than control participants, i.e. a larger difference in the ratings between all congruent and incongruent trials (inclusion as well as exclusion bias).

H4.2: While judging their own emotional state, ASD participants will show a higher AB than control participants, that is a larger difference in the rating between all congruent and incongruent trials.

H5: Overall, both groups will show an EEB as well as an AB, that is, a difference in ratings between congruent and incongruent trials, with the EEB being of a greater size than the AB. Both biases will be accompanied by enhanced hemodynamic activity in the rTPJ and the rSMG.

3 Methods

3.1 Study design

To induce feelings of social pain, we selected the “Cyberball paradigm” (originally developed by Williams et al., 2000), a mock-interactive virtual ball tossing game in which feelings of social inclusion or exclusion can be induced by manipulating the amount of ball tosses a player receives (i.e. whether he or she is included or excluded by the other players) The relevant players’ feelings are then judged on a scale from negative to positive. The Cyberball game used for this study, a modified version of the one used by Novembre et al. (2015), was developed specifically for the use with autistic participants and validated in a pilot study (Stepnicka, 2016). It uses videos of real people (instead of cartoon characters) to ensure a higher level of ecological validity, while at the same time minimizing possible distracting elements such as frequent cuts. For this study, the game consisted of three distinct runs which made up the different experimental conditions, and thus differed slightly from each other in two key aspects: the participant was either an active player or an observer, and would either be asked to rate his or her own emotional state or that of the player standing opposite them. All three conditions consisted of 16 blocks of ball-tossing with about 13-15 ball throws per block and a rating session after each block (see Figure 1 for a schematic representation of the procedure).

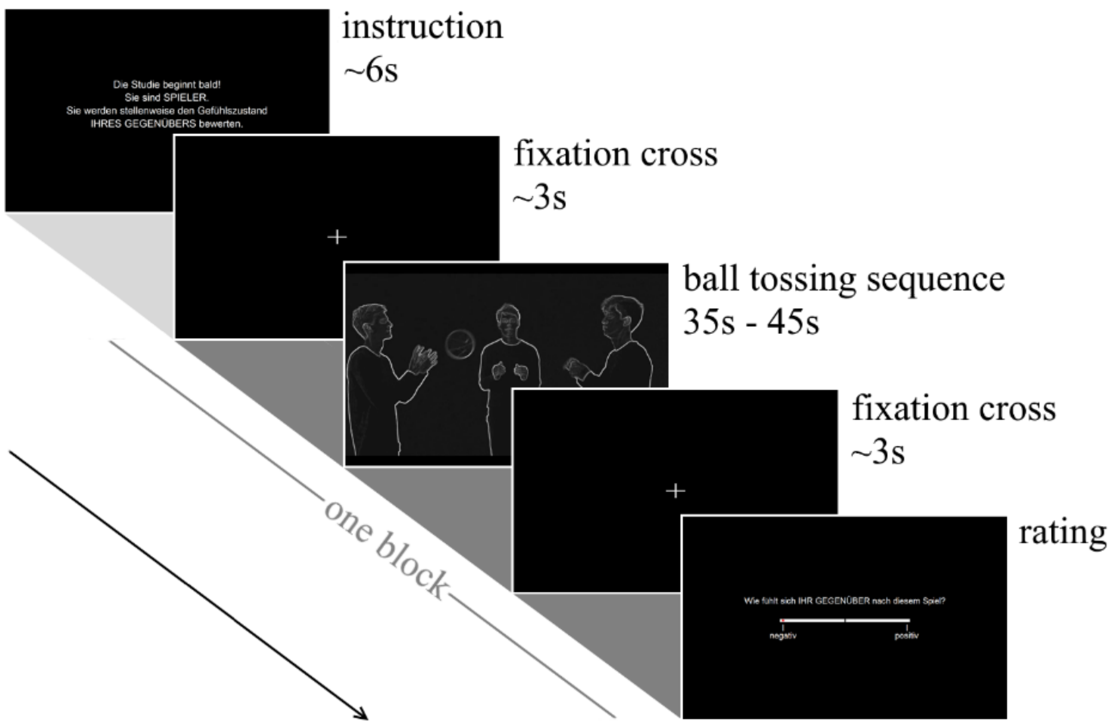

Figure 1. Schematic depiction of one block of the cyberball game.

The blocks presented a systematic variation of inclusion and exclusion of both the player and the person opposite, creating congruent situations (when both were either being included or excluded) and incongruent situations (when one was being included and the other excluded). Figure 2 shows the order and characteristics of different blocks for all conditions.

Double Self		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	Self	**IN**	**IN**	**IN**	**IN**	**EX**	**EX**	**EX**	**EX**	**IN**	**IN**	**IN**	**IN**	**EX**	**EX**	**EX**	**EX**
	Other	IN	IN	EX	EX	EX	EX	IN	IN	IN	IN	EX	EX	EX	EX	IN	IN

Double Other Active		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	Self	IN	IN	IN	IN	EX	EX	EX	EX	IN	IN	IN	IN	EX	EX	EX	EX
	Other	**IN**	**IN**	**EX**	**EX**	**EX**	**EX**	**IN**	**IN**	**IN**	**IN**	**EX**	**EX**	**EX**	**EX**	**IN**	**IN**

Double Other Passive		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	Self	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
	Other	**IN**	**IN**	**EX**	**EX**	**EX**	**EX**	**IN**	**IN**	**IN**	**IN**	**EX**	**EX**	**EX**	**EX**	**IN**	**IN**

Figure 2. Order and valence for all 16 blocks of each conditions. The rating target (self or other) for each condition is shown in boldface type. Congruent trials have a yellow background. IN = Inclusion, EX = Exclusion, O = Observer (i.e. not playing)

In the first condition, *Double Self* (DS), participants were asked to throw a ball around with three other players, whose avatars they could see on a screen before them (see Figure 3). They were informed that these avatars were controlled by real other players, when in fact the sequence of ball tosses was mostly predetermined (except for the decisions the players themselves made). During the rating session, they were asked to rate the state of their own feelings by moving a cursor on a scale from “Negative” to “Positive”, giving a rating in the range from -10 (very negative) to +10 (very positive). The second condition, *Double Other Active* (DOa), was identical to DS, except that participants were now always asked to rate the feelings of the player standing opposite them. During the third condition, *Double Other Passive* (DOp), players were once again instructed to judge the emotional state of the person across from them, except that during this condition, they did not actively take part in the game, and instead were only an observer watching four other people play the game through a first-person perspective. The three conditions were presented in a counterbalanced order, and the ball-tossing blocks within each condition were pseudorandomized.

a. b.

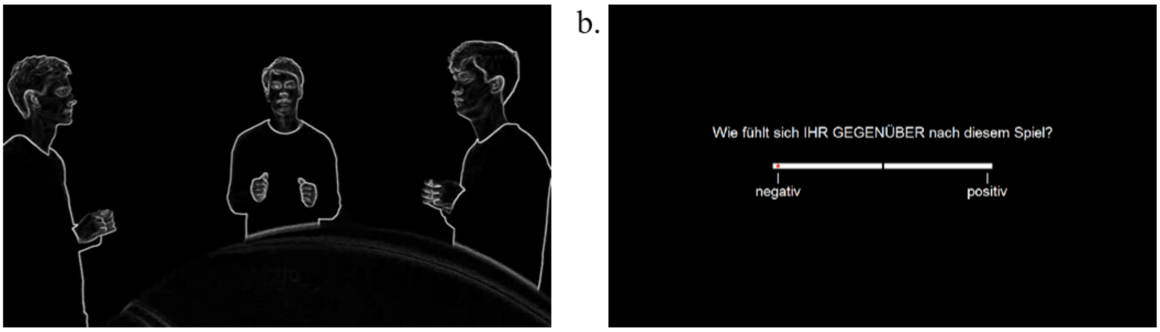

Figure 3. Sample screenshots of the DOa game condition. 3a. View the participant had during the ball tossing sequence (currently holding the ball). 3b. Rating Screen reading "How does the PERSON OPPOSITE YOU feel after this game?"

Participants were instructed that they themselves, as well as the player opposite, could only throw the ball to the left or the right, while the other two players could also throw straight ahead (i.e. to each other). This was done to ensure that the exclusion of the opposite player could not be interrupted by the participants and conversely, that the participants did not develop any negative feelings towards the opposite player when they themselves were being excluded (being aware that that person could also not pass them ball to them). Since the game the participants were playing was not truly interactive, no actual other players were involved. However, to ensure that true feelings of social exclusion were induced, each testing session included four confederates who had been instructed to act like regular naïve participants, playing the game from computers. Four was chosen as the minimum number necessary so that for each game, four people could be actively playing and one could be the observer. All confederates were volunteers: some were psychology students who were interested in learning about fMRI studies, and some were friends and acquaintances of the experimenters.

3.2 fMRI Data Acquisition and General Procedure

Testing took place at the School of Dentistry (Universitätszahnklinik) of the Medical University of Vienna. A 3 Tesla MAGNETOM Skyra MRI system (Siemens Healthcare GmbH, Erlangen, Germany) equipped with a 32-channel head coil was used to collect gradient echo planar T2-weighted MRI images with blood oxygenation level-dependent (BOLD) contrast as well as T1-weighted anatomical images. The multiband echo planar imaging (EPI) sequence was specified to the following parameters: interleaved acquisition, echo time (TE)/repetition time (TR) = 34/704 ms, 32 axial slices, voxel size = 2.2×2.2×3.5 mm, flip angle = 50°, field of view = 210 mm, and matrix size = 96×96. The number of volumes per condition varied with the length of the game but consisted of ~1000 volumes per run. Structural images were acquired with a rapid gradient echo sequence with the following parameters: TE/TR = 2.29/2300 ms, 176 sagittal slices, voxel size = 0.9×0.9×0.9 mm, flip angle = 8°, and field of view = 240 mm.

Testing appointments were arranged individually with each participant per his or her availability, but usually took place in the late afternoon or evening. To ensure that all participants were adequately apprised of the risks of functional magnetic resonance imaging, they were sent an email with general information on the study and on fMRI safety prior to their appointment. The email also informed participants that they would be playing a virtual game with four other people, but that they would be the only ones in the scanner. Participants were also asked not to consume any drugs (other than necessary daily medication) or alcohol in the 24 hours before the study. On the day of testing, all "participants" (i.e. the actual subject and four confederates) were met by the experimenter at the main entrance of the dental clinic and taken to the anteroom of the scanner. There, all participants were given the study information as well as consent forms to sign. Additionally, the test subject was given an fMRI security questionnaire and consent form, and was briefed on possible risks and side effects. For privacy reasons, this was done in a separate room, while a second experimenter supervised the confederates. Afterwards, all players were asked to sit in a circle of chairs (to enhance the social situation) and instructed on how to play the game. They were then assigned to individual computers and given the opportunity to play two short test rounds of the game.[3] Thus, the actual subject got a chance to play one round of both the active and the passive condition and any uncertainties could be resolved before the person was in the scanner. After being asked to take off any metal objects or electronic devices, the participant was then escorted into the scanner room and instructed on how to use the response box as well as the alarm button. He or she was given noise-reducing earplugs and was made as comfortable as possible on the scanner bed. All participants were instructed to lie as still as possible and to alert the experimenters immediately if they felt any pain or discomfort. Figure 4 shows a schematic depiction of the participant's position in the scanner.

[3] It should be noted that two ASD participants were tested in a slightly modified setup: due to a lack of confederates, they were told that the other participants were playing the game from the University's computer lab and were connected to them via the Internet. To mitigate any negative effects, they were matched with two controls subjects who also received these modified instructions.

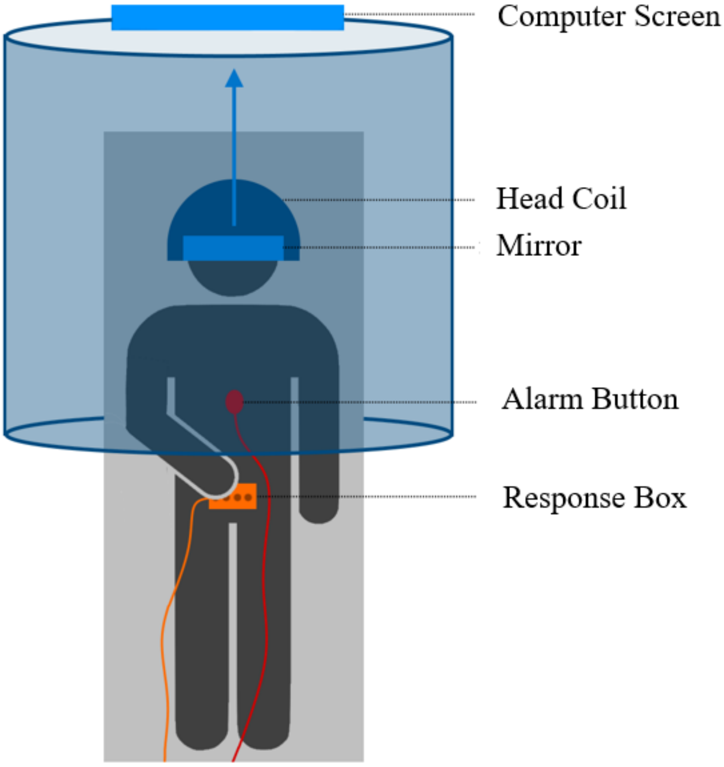

Figure 4. Schematic depiction of a participant's position in the scanner.

The experimenter then turned off the lights and left the scanner room. At this point, the confederates were asked to leave and one more test round was played so the participant could practice using the buttons on the response box. Initial scanning adjustments (i.e. head localization, shimming) took about 5-7 minutes, then the participant played the three games (DS, DOa, DOp) in counterbalanced order, with short breaks in between, during which the experimenter communicated with the participant via the intercom. In the end, the participant was given a relaxing video of mountain scenery to watch while the structural image was acquired. A participant's total time in the scanner lasted about 50 to 60 minutes. Subsequently, the participant was asked to fill out the questionnaires, which took about 45-60 minutes. Lastly, all participants were paid 25 Euros monetary compensation and given a thorough debriefing by the two experimenters, which included information about the goal of the study as well as the manipulation (i.e. that the confederates had not been real participants and that the game had been predetermined).

3.3 Participants

All subjects were recruited and tested between September 2016 and February 2017. Neurotypical control participants were recruited via printed flyers, personal email invitations and advertisement on social media, as well as the University's research recruitment tool

“Laboratory Administration for Behavioral Sciences” (LABS). Prerequisites for inclusion in the study comprised being 18 years of age or older, having German as a first language, not currently suffering from any neurological or psychiatric disorder, never having studied psychology, never having participated in a similar research project, and not having any fMRI risk factors. These criteria were assessed with an online questionnaire (and additional follow-up questions per email, if necessary) before participants were invited to the study. To avoid confounding variables, only right-handed men were included in Study 1, however, female and left-handed controls were recruited specifically to match individual ASD participants for Study 2. Autistic subjects were recruited separately through a database of people who had previously participated in autism research. Additionally, advertisements were placed on autism related online forums and social media groups, and emails were sent to Viennese organizations that work with people with ASD. To be included in the ASD group, participants had to have a diagnosis of Asperger syndrome (ICD: F84.5, DSM: 299.80) provided by a clinical psychologist or psychiatrist. Six participants had to be excluded from the data analysis due to malfunctions during data collection and data transfer, claustrophobia during scanning or very low scores on the intelligence measures. Two additional subjects from Study 1 had to be excluded from the fMRI analysis only, because excessive movement during scanning created large artefacts in the neuroimaging data. This led to a total sample of $N = 39$ participants (37 for the fMRI analysis).

Sample Study 1. The sample for Study 1 consisted of $n_1 = 20$ right-handed healthy adult men. The mean age was 32.95 years (SD = 8.52), ranging from 20 to 48 years of age. All participants spoke German as their first language. 10% of participants had an apprenticeship as their highest level of education, while 35% possessed a high school diploma and 55% a university degree. Only one participant reported having had a psychiatric disorder in the past (depression) and none of the participants were currently taking any regular medication. All participants reported having a computer at home and using it daily (40%) or several times a day (60%). Sample characteristics demographic information can be found in Table 2.

Sample Study 2. For Study 2, 15 ASD participants were matched with 15 neurotypical control subjects by age, sex, handedness and intelligence scores, leading to a total sample of $n_2 = 30$. Each group consisted of 13 men (86.7%) and 2 women (13.3%). One male subject in each group (6.67%) was left-handed. All participants spoke German as their first language. The two groups differed significantly in their autistic traits ($t_{(28)} = -7.265$, $p < .001$), as well as their level of alexithymia on all three subscales (see Table 2) and on the *Perspective Taking* subscale of the empathy questionnaire ($t_{(28)}$ = -3.006, p < .05). Table 2 shows the comparison of sociodemographic data and matching characteristics.

Table 2

Sample characteristics and matching criteria for Study 1 and Study 2.

Characteristics	Study 1	Study 2			
		ASD	Controls	$t_{(28)}$	p
Sample Size	20	15	15		
Age	32.95 (8.52)	37.20 (10.84)	37.33 (11.09)	0.033	.974
Intelligence Scores					
SPM	7.70 (1.33)	7.60 (1.24)	7.27 (2.01)	-0.545	.590
MWT	28.65 (4.42)	29.00 (4.12)	29.33 (3.99)	0.225	.842
Autistic Traits	6.75 (4.75)	23.73 (6.39)	8.00 (5.43)	-7.265	< .001
Depression	6.85 (7.32)	12.93 (10.55)	6.87 (7.75)	-1.796	.083
Trait Empathy					
Fantasy	3.04 (0.64)	2.49 (0.77)	3.09 (0.73)	2.186	.037
Empathic Concern	3.55 (0.63)	3.23 (0.75)	3.58 (0.75)	1.293	.207
Perspective Taking	3.61 (0.47)	2.99 (0.72)	3.68 (0.52)	3.006	.006
Personal Distress	2.49 (0.55)	3.00 (0.80)	2.57 (0.55)	-1.729	.095
Alexithymia					
Difficulty Identifying Feelings	12.75 (5.27)	20.60 (5.96)	12.33 (4.85)	-4.166	<.001
Difficulty Describing Feelings	12.45 (3.86)	18.40 (3.16)	12.27 (3.65)	-4.919	< .001
Externally Oriented Thinking	17.00 (4.38)	20.53 (4.58)	16.60 (4.07)	-2.487	.019
Education					
Apprenticeship	10.0%	20.0%	13.3%		
AHS/BHS without Matura	-	6.7%	-		
AHS/BHS with Matura	35.0%	33.3%	13.3%		
University	55.0%	40.0%	73.3%		

(continued)

Characteristics	Study 1	Study 2			
		ASD	Controls	$t_{(28)}$	*p*
Occupation					
Student	35.0%	20.0%	20.0%		
Employed	50.0%	60.0%	60.0%		
Self-employed	10.0%	-	6.7%		
Retired	-	6.7%	6.7%		
Unemployed	5.0%	13.3%	6.7%		
Regular Medication					
Yes	-	20%	6.7%		
No	100%	80%	93.3%		
Computer Experience					
Beginner	-	6.7%	6.7%		
Advanced	45%	33.3%	40.0%		
Expert	55%	60.0%	53.3%		

Note. Means (standard deviations) are given for age, intelligence scores, autistic traits, depression, trait empathy, and alexithymia scores. Other demographic characteristics are shown in percentages. SPM = Standard Progressive Matrices; MWT = Mehrfachwahl-Wortschatz-Intelligenztest; AHS = Allgemein bildende höhere Schule; BHS = berufsbildende höhere Schule. See section 4.4 for an explanation of the demographic measures used.

3.4 Questionnaires

Intelligence. Two short versions of intelligence measures were presented to the participants to match the ASD group with the control group. The Standard Progressive Matrices (SPM; Raven, 2000) is a non-verbal tool to assess general intelligence. Each item consists of a figural diagram with an incomplete pattern, for which participants had to choose the correct component out six options. Because nine items were used in this case, participants' scores could range between a total of zero and nine points. For internal consistency, the full-length version of the SPM has a Cronbach's α > .90. The Mehrfachwahl-Wortschatz-Intelligenztest (MWT-B; Lehrl, 1999) is a multiple-choice lexical intelligence test that measures recognition vocabulary. For each of the 37 items, participants were asked to identify the genuine word out of line of made-up words. The MWT-B has a criterion validity of r = .72.

Alexithymia. The German 20-item version of the Toronto Alexithymia Scale (TAS-20; Taylor, Bagby, & Parker, 2003) was used to measure for symptoms of alexithymia. This self-report questionnaire contains 20 items that can be answered on a five-point Likert scale from 1 meaning "Does not apply at all" to 5 meaning "applies absolutely" and can be categorized into three subscales (Difficulty Identifying Feelings, Difficulty Describing Feelings and

Externally-Oriented Thinking). An example item is “It is often unclear to me what I am currently feeling”. The internal reliability for the overall scale shows a Cronbach’s Alpha of .78.

State Empathy. The Interpersonal Reactivity Index, or IRI (Davis, 1983) is a multi-dimensional construct to measure both cognitive and affective aspects of state empathy. Its 28 items can be answered on a 5-point Likert scale ranging from “Never” to “Always”. The IRI is divided into four subscales, three of which measure emotional empathy (*Fantasy, Empathic Concern*) and *Personal Distress*) and one measuring cognitive empathy (*Perspective Taking*). An example item is “I often have tender, concerned feelings for people less fortunate than me”. The subscales have internal reliability subscales ranging from Cronbach’s α = .70 to .78.

Autistic Traits. To assess symptom severity, the shortened German version (Freitag et al., 2007) of the original Adult Autism-Spectrum Quotient (AQ; Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001) was used. This self-report screening questionnaire asks respondents to rate items describing themselves on a four-point scale ranging from “I definitely agree” to “I don’t agree at all”. An example for an item is “I prefer doing things the same way over and over again”. The three subscales have internal consistencies ranging from Cronbach’s α = .65 to .78. Individuals can score in the range from 0-33 (one point per item) and the clinically relevant cut-off value was determined to be 17; though it should be noted that the instrument should not be used for diagnostic purposes (Freitag et al., 2007).

Symptoms of Depression. To assess and control for depressive symptoms in the participants, the German version of the Beck’s Depression Inventory – Second Edition (BDI-II; Kühner, Bürger, Keller, & Hautzinger, 2007) was used. This questionnaire consists of 21 items, each measuring a symptom of clinical depression with four statements describing increasing severity of the symptom on a scale of zero to three. Participants were asked to recall their feelings during the last two weeks and to mark the sentence that best describes their emotional state. For example, the item “Sadness” consists of the following statements: “0 – I do not feel sad.”, “1 – I am often sad.”, “2 – I am sad all the time.” and “3 – I am so sad and unhappy that I can’t stand it.”. The Cronbach’s α for the internal consistency of the BDI-II were $\geq$ .84 for both clinical and non-clinical samples. The clinically relevant cut-off scores are 9-13 points for no or minimal depression, 14-19 points for mild depression, 20-28 points for moderate depression and $\geq$ 29 points for severe depression.

Sociodemographic Data. All participants were also given a short questionnaire asking for information about the participants' age, nationality, sex, handedness, highest level of education, occupation, level of monthly income, living situation, marital status, use of psychoactive medication, neurological and psychiatric disorders, computer use and computer skill level as well experience with computer games.

Paradigm Believability. During debriefing, participants were asked how much they had felt involved in a game with other people. This was done as a manipulation check to assess the possibility that a subject may realize that they were in fact playing a game with a predetermined sequence of inclusion and exclusion and therefore may not feel social pain during exclusion trials. If the participants mentioned suspecting that they had not been playing with real other people, they were asked from which point on they had felt suspicious of the paradigm and whether they still had been emotionally involved in the game.

3.5 Statistical Analysis

The behavioral (i.e. rating) data was acquired with and extracted via MATLAB 7.10.0 (R2010a) and the statistical analysis was performed using the statistical software for the social sciences (SPSS 22), using a general linear model (GLM) approach. For Study 1, a three-factorial repeated measures ANOVA was calculated. The three within-subject factors each comprised two levels (2x2x2): *Target* (Double Self versus Double Other Active), *Valence* (Inclusion versus Exclusion) and *Congruency* (Congruent versus Incongruent). The original third target condition of the experiment (Double Other Passive) was used in a different thesis and was therefore not included in the calculation for this study. For simplicity, the "Double Other Active" condition will be referred to as "Double Other" from here on out. For Study 2, a four-factorial mixed ANOVA (2x2x2x2) was used. In addition to the three within-subject factors from Study 1, a *group* factor with two levels (Control versus ASD) was calculated. Additionally, two-sided Spearman correlations were calculated for both studies to investigate the associations between the mean AB, EEB and individual levels of alexithymia, trait empathy and autistic traits (as measured by self-report questionnaires).

3.6 Functional Analysis

Brain imaging data were analyzed with SPM12 (Wellcome Trust Centre for Neuroimaging, University College London) running on MATLAB 7.10.0 (R2010a). For pre-processing, slice-time correction was applied using the first slice as a reference. All functional volumes were realigned to the mean functional image of each session and each subject's structural image was co-registered to the first functional image. Images were then segmented into tissue type, normalized to the individual's structural image, and smoothed by convolution with an 8mm full-width at half-maximum (FWHM) Gaussian kernel. Each participant's data was checked for motion artifacts. As mentioned in section 4.3, two additional subjects had to be excluded from the fMRI analysis at this point because their movement parameters exceeded a limit of ±2 mm movement and ±2 degrees of rotation.

Following pre-processing, data were analyzed using the general linear model framework in a block-design. During first-level analysis, two separate first-level regressors (video duration and rating duration) were defined for each valence-level (Inclusion and Exclusion) and each congruency-level (Congruent and Incongruent) for a total of eight regressors for each of the three games (Self, Other-Active, Other-Passive) for each subject. Additional regressors included the realignment parameters and all regressors were convoluted with a canonical hemodynamic response function (interscan interval: .704). For the second-level analysis a full-factorial design with three within subject factors (for Study 1 and 2) and one between-subjects factor (for Study 2 only) was calculated. No masking or p-value adjustment were applied (the threshold for uncorrected significance was set at $p = .001$), though a cluster-extend based threshold of $k \geq 10$ voxels was used. The MRIcron software package (Rorden et al., 2007) was used for anatomical interpretation.

4 Results

4.1 Behavioral Results Study 1

Table 3 shows the mean ratings and standard deviations of all 20 participants for the different trials in the two target conditions (Double Self and Double Other). Note that in the trial name (e.g. IN/IN, IN/EX) the first two letters denote the state of the player themselves, while the second two letters denote the state of the opposite person. Relevant inclusion and exclusion trials differ depending on who the target of the rating is. For example, during the Double Self sequence (i.e. judging one's own feelings), the third and fourth trials (EX/EX and EX/IN) are the exclusion trials, while during the Double Other sequence (i.e. judging the other person's feelings), the second and third trials (IN/EX and EX/EX) are the exclusion trials.

Table 3
Means and standard deviations for types of trial and biases for both target sequences.

Target condition	Trial (S/O)	M (SD)	Valence bias	M (SD)	Overall bias	M (SD)
DS	IN/IN	5.11 (3.29)	Exclusion Bias	3.94 (3.90)	AB	2.97 (3.14)
	IN/EX	1.17 (2.20)				
	EX/EX	-5.23 (3.55)	Inclusion Bias	1.99 (3.78)		
	EX/IN	-3.23 (3.73)				
DO	IN/IN	4.69 (3.46)	Exclusion Bias	1.42 (4.27)	EEB	1.35 (2.39)
	IN/EX	-3.85 (4.08)				
	EX/EX	-5.13 (3.70)	Inclusion Bias	1.28 (3.96)		
	EX/IN	3.26 (4.00)				

Note. To calculate the biases, the absolute values of the trial means were used. The Exclusion Bias was calculated by subtracting IN/EX from IN/IN (for DS) and EX/IN from IN/IN for DO. The Inclusion Bias was calculated by subtracting EX/IN from EX/EX (for DS) and IN/EX from EX/EX for DO. The Overall Bias was calculated as the mean of the Inclusion and Exclusion biases. DS = Double self; DO = double other; S = Self; O = Other; IN = Inclusion; EX = Exclusion; AB = Altercentric Bias, EEB = Emotional Egocentricity Bias.

During the Double Self condition, participants rated themselves more negatively when the other person was being excluded (Exclusion Bias) and more positively when the other person was being included (Inclusion Bias). In other words, their ratings showed an overall shift towards the state of the other person in incongruent trials (Altercentric Bias). Conversely, during the Double Other condition, participants rated the other person more negatively when they themselves were being excluded (Exclusion Bias) and more positively when they themselves were being included (Inclusion Bias). In assessing the other person, the ratings showed an overall shift towards the rater's own feelings (Emotional Egocentricity Bias). For a graphical depiction, see Figure 5.

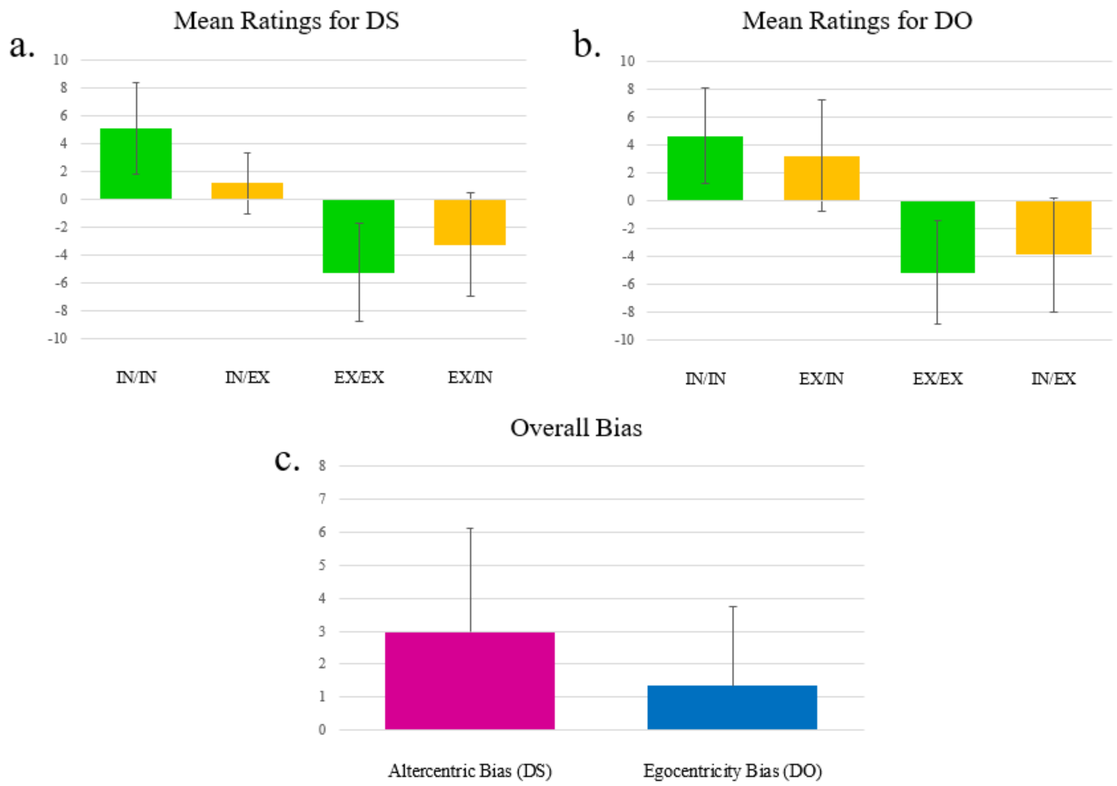

Figure 5. Plot of mean rating values and standard deviations for the (a) Double Self condition and (b) Double Other condition. Congruent trials are shown in green, incongruent trials in orange. To calculate the overall bias for each condition (c) incongruent trials were subtracted from congruent trials. DS = Double Self; DO = Double Other.

To calculate the degree of empathic judgements in the two different target conditions (Double Self and Double Other), a three-factorial (2 x 2 x 2) repeated measures ANOVA (GLM) was used. Because only the absolute values and not the direction of the bias (negative or positive) was of interest for this study, all negative (i.e. exclusion) trials were multiplied by -1 prior to analysis, ensuring all trial means had a positive sign and were thus comparable. A significant main effect of congruency was found ($F_{(1,19)} = 21.510$, $p = < .001$, $\eta_p^2 = 0.531$) meaning there was a significant average difference between congruent and incongruent trials (congruent – incongruent: (*M*/*SE*) = 2.16/0.47; $p < .001$) with participants rating less extremely during incongruent trials (*M*/*SE*) = 2.88/0.50) than congruent trials (*M*/*SE*) = 5.04/0.50). That is, during incongruent trials, participants' ratings were drawn towards the emotional state of the person not currently being rated. This supports the existence of an AB (in the case of the Double Self condition) as well as an EEB (in the Double Other condition). No other main effects or interaction effects were significant (Target, $F_{(1,19)} = 3.747$, $p = .068$, $\eta_p^2 = 0.165$; Valence, $F_{(1,19)} = 1.020$, $p = .325$, $\eta_p^2 = 0.051$; Target x Valence, $F_{(1,19)} = 0.365$, $p = .553$, $\eta_p^2 = 0.019$; Target x Congruency, $F_{(1,19)} = 3.754$, $p = .068$, $\eta_p^2 = 0.165$; Valence x Congruency, $F_{(1,19)} = 0.874$, $p = .362$, $\eta_p^2 = 0.044$; Target x Valence x Congruency, $F_{(1,19)} = 2.255$, $p = .150$, $\eta_p^2 = 0.106$). This indicates that ratings were neither influenced by whether the rater was in a positive or negative feeling state, nor by the target of the ratings; although the interaction Target x Congruency came close to significance, indicating a trend towards a difference in size between the AB and EEB (AB (*M/SE*) = 2.97/3.14), EEB (*M/SE*) = 1.35/2.39). The lack of a three-way interaction suggests that the AB and the EBB were of similar sizes irrespective of the emotional state they were caused by (DS: Inclusion Bias (M/SE) = 1.99/3.78, Exclusion Bias (*M/SE*) = 3.94/3.90; DO: Inclusion Bias (M/SE) = 1.28/3.96, Exclusion Bias (*M/SE*) = 1.42/4.27). To investigate the association between the mean AB, EEB and individual levels of alexithymia, trait empathy and autistic traits, two-sided Spearman correlations were calculated. No significant associations were found between the biases and any of the scales, however, there was a significant correlation between autistic traits and the *Perspective Taking* scale of the empathy questionnaire ($r_s = .564$, $p = .002$) as well as the *Externally Oriented Thinking* scale of the Alexithymia questionnaire ($r_s = .791$, $p = .002$). All correlations can be found in Table A1 in the supplementary material.

4.2 Neuroimaging Results Study 1

Sample size for the fMRI analysis of Study 1 consisted of 18 adult neurotypical males. Only the main effects and interactions relevant for the hypotheses are included.

Main effect of experiment. The main effect of experiment shows the overall effect the experiment had on the participants compared to a baseline, constituting a manipulation check. The whole-brain contrast for playing the Cyberball game versus a baseline revealed enhanced hemodynamic activity in the following regions: right middle temporal gyrus, bilateral calcarine cortex, and left middle occipital gyrus. (see Table 4).

Table 4

Main effect of experiment (Game > Baseline).

						Coordinates [mm]		
H	Anatomical region	Cluster K	*p* (unc)	*T*	Z-score	x	y	z
R	Middle temporal gyrus	1060	< .001	12.27	Inf	50	-70	4
R	Calcarine cortex	1859	< .001	10.81	Inf	8	-92	12
L	Calcarine cortex		< .001	10.21	Inf	-2	-96	4
L	Calcarine cortex		< .001	9.95	Inf	-8	-92	10
L	Middle occipital gyrus	759	< .001	9.11	Inf	-46	-72	4

Note. H = Hemisphere, R = Right hemisphere, L = Left hemisphere.

Main effect of target. The main effect of target shows the comparison of the hemodynamic responses between the two target conditions Double Self and Double Other, i.e. being asked to judge the emotions of oneself self or those of the other person. Comparing the DO condition to the DS condition (*Other* > *Self*), no significant clusters of increased activity were found. However, the following regions showed enhanced neural activity during the self-rating in comparison to the other rating (*Self* > *Other*): right superior temporal pole and right putamen (*Self* > *Other*; see Table 5).

Table 5
Main effect of target (Self > Other).

						Coordinates [mm]		
H	Anatomical Region	Cluster K	*p* (unc)	*T*	Z-score	x	y	z
R	Superior temporal pole	29	< .001	4.07	3.95	46	16	-22
R	Putamen	29	< .001	3.73	3.63	30	-18	4

Note. H = Hemisphere, R = Right hemisphere, L = Left hemisphere.

Main effect of valence. This shows the comparison of the hemodynamic responses between the inclusion and the exclusion trials irrespective of target or congruency. During the inclusion trials, the following regions showed enhanced activity when compared to the exclusion trials (*Inclusion* > *Exclusion*): right middle temporal gyrus, left median cingulate gyrus, left superior frontal gyrus, left supplementary motor area, bilateral cerebellum, bilateral insula, right opercular inferior frontal gyrus, and right fusiform gyrus (see Table 6 and Figure 7).

Table 6
Main effect of valence (Inclusion > Exclusion).

						Coordinates [mm]		
H	Anatomical Region	Cluster K	*p* (unc)	*T*	Z score	x	y	z
R	Middle temporal gyrus	996	< .001	5.36	5.10	56	-64	8
L	Median cingulate gyrus	281	< .001	4.52	4.36	-10	14	44
L	Superior frontal gyrus		< .001	4.12	3.99	-24	0	48
L	Supplementary motor area		< .001	4.00	3.88	-8	8	52
L	Cerebellum crus I	50	< .001	3.81	3.71	-38	-52	-36

(continued)

H	Anatomical Region	Cluster K	*p* (unc)	*T*	Z score	Coordinates [mm]		
						x	y	z
R	Cerebellum	17	< .001	3.53	3.45	40	-52	-34
L	Insula	57	< .001	3.73	3.63	-36	20	6
R	Insula	56	< .001	3.72	3.62	34	24	10
R	Opercular inferior frontal gyrus	77	< .001	3.57	3.48	50	16	18
R	Fusiform gyrus	15	.001	3.34	3.27	28	-62	-8

Note. H = Hemisphere, R = right Hemisphere, L = Left hemisphere.

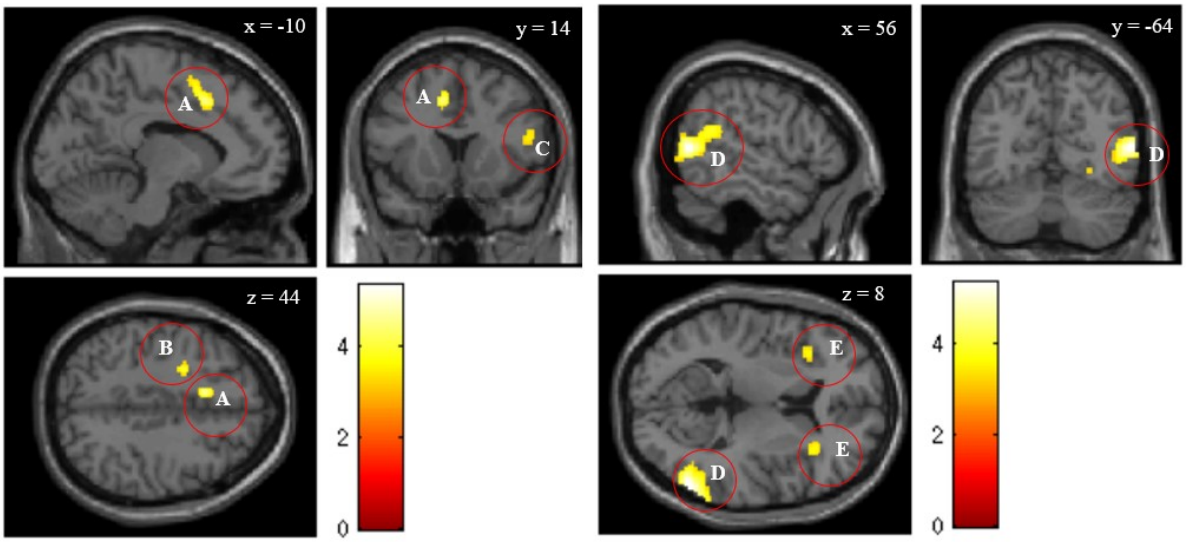

Figure 6. Regions of enhanced activation for the main effect of valence (Inclusion > Exclusion): (A) left median cingulate gyrus, (B) left superior frontal gyrus, (C) right opercular inferior frontal gyrus, (D) right middle temporal gyrus and (E) bilateral insula.

Comparing situations of social pain (i.e. exclusion trials) to situations of social inclusion, the following regions showed enhanced hemodynamic activity (*Exclusion > Inclusion*): Bilateral postcentral gyrus, right precentral gyrus, left paracentral lobule, and left calcarine cortex (see Table 7).

Table 7

Main effect of valence (Exclusion > Inclusion).

H	Anatomical Region	Cluster K	*p* (unc)	*T*	Z score	Coordinates [mm]		
						x	y	z
R	Postcentral gyrus	428	< .001	5.08	4.85	28	-36	68

(continued)

H	Anatomical Region	Cluster K	*p* (unc)	*T*	Z score	Coordinates [mm]		
						x	y	z
L	Postcentral gyrus	152	< .001	4.30	4.15	-22	-34	68
R	Precentral gyrus		< .001	5.04	4.82	22	-22	68
L	Paracentral lobule		< .001	4.00	3.88	-20	-26	68
L	Calcarine cortex	91	< .001	3.91	3.80	-4	-90	-6

Note. H = Hemisphere, R = Right hemisphere, L = Left hemisphere.

Main effect of congruency. This contrast calculates the differences in neural activation between congruent and incongruent trials independent of target or valence, in order to investigate the existence of an overall bias (EEB and AB). Table 8 shows the difference between the neural activity during congruent trials compared to incongruent trials (*Congruent* > *Incongruent*), which revealed greater activation in the bilateral lingual gyrus. During incongruent trials, there was increased activity in the right middle temporal gyrus, the right superior temporal gyrus, and the right precuneus cortex compared to congruent trials (*Incongruent* > *Congruent*, see Table 9 and Figure 7).

Table 8

Main effect of congruency (Congruent > Incongruent).

H	Anatomical Region	Cluster K	*p* (unc)	*T*	Z score	Coordinates [mm]		
						x	y	z
L	Lingual gyrus	241	< .001	4,42	4,26	-14	-60	-2
R	Lingual gyrus	247	< .001	3,84	3,74	16	-56	2

Note. H = Hemisphere, R = Right hemisphere, L = Left hemisphere.

Table 9

Main effect of congruency (Incongruent > Congruent).

H	Anatomical Region	Cluster K	*p* (unc)	*T*	Z score	Coordinates [mm]		
						x	y	z
R	Middle temporal gyrus	37	< .001	3,57	3,48	50	-66	10
R	Superior temporal gyrus	20	< .001	3,47	3,39	54	-40	12
R	Precuneus cortex	10	.001	3,29	3,22	4	-52	56

Note. H = Hemisphere, R = Right hemisphere, L = Left hemisphere.

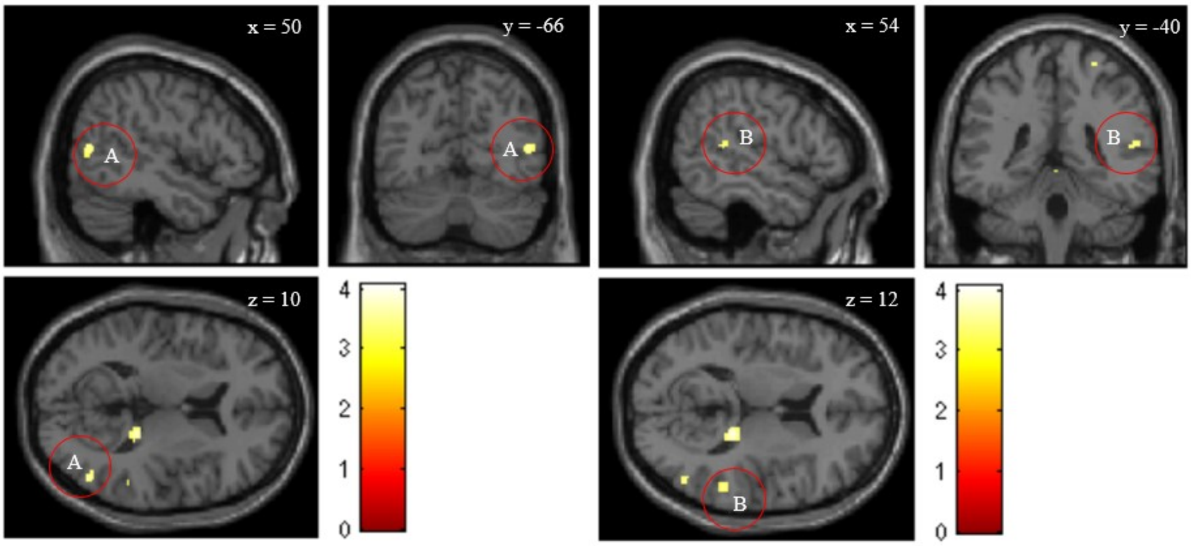

Figure 7. Regions of enhanced activation for the main effect of congruency (Congruent > Incongruent): (A) right middle temporal gyrus, (B) right superior temporal gyrus.

Interaction effect of target and congruency. This interaction effect describes the difference in the hemodynamic responses between the self-rating and other-rating (i.e. the Double Self versus the Double Other condition) for the contrast incongruent versus congruent. In other words, it compares the AB to the EEB. This effect was not significant in the behavioral data, although there was a trend. When comparing AB (*Self (Incongruent > Congruent*) to the EEB (*Other (Incongruent > Congruent*), the following regions showed increased activation: right middle occipital gyrus, left thalamus, right precentral gyrus, bilateral putamen, right superior parietal gyrus, as well as right calcarine cortex (see Table 10 and Figure 8).

Table 10

Interaction effect of target x congruency (Self (Incongruent > Congruent) > Other (Incongruent > Congruent)).

						Coordinates [mm]		
H	Anatomical Region	Cluster K	*p* (unc)	*T*	Z score	x	y	z
R	Middle occipital gyrus	136	< .001	4.03	3.91	40	-78	28
R	Middle occipital gyrus	45	< .001	3.52	3.44	36	-64	36
R	Middle occipital gyrus		0.001	3.23	3.16	40	-64	26
L	Thalamus	24	< .001	3.77	3.67	-16	-26	8
R	Precentral gyrus	59	< .001	3.56	3.48	36	4	52
R	Putamen	28	< .001	3.50	3.41	24	22	2

(continued)

H	Anatomical Region	Cluster K	*p* (unc)	*T*	Z score	Coordinates [mm]		
						x	y	z
R	Putamen	12	0.001	3.31	3.24	30	-2	8
L	Putamen	14	< .001	3.47	3.39	-28	-4	4
L	Putamen	16	< .001	3.42	3.35	-22	6	12
R	Superior parietal gyrus	55	< .001	3.49	3.41	20	-76	52
R	Calcarine cortex	19	.001	3.34	3.27	8	-70	60

Note. H = Hemisphere, R = Right hemisphere, L = Left hemisphere.

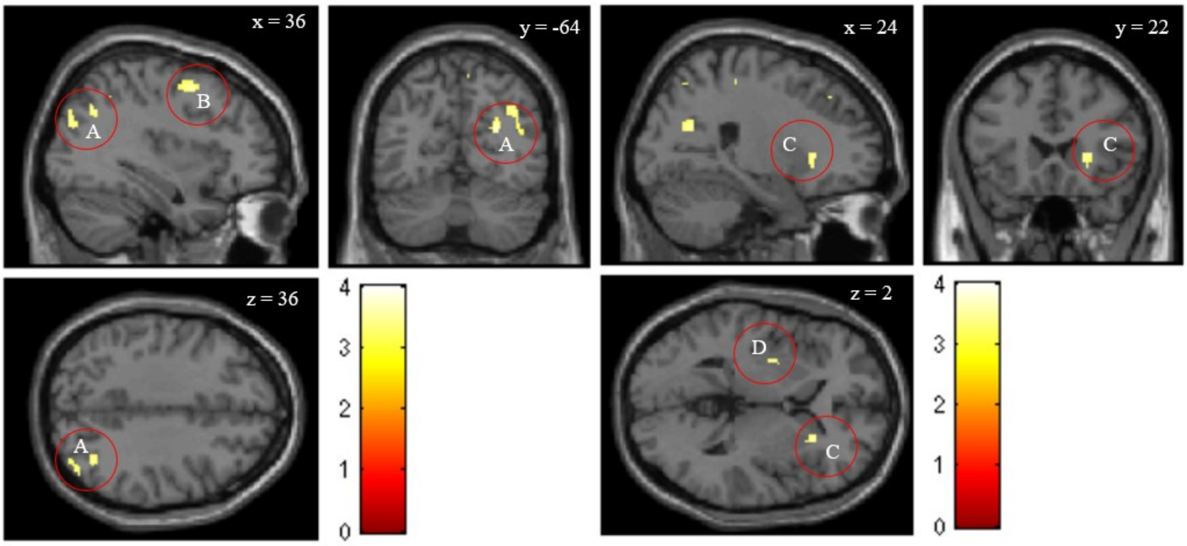

Figure 8. Regions of enhanced activation for the interaction effect of target and congruency (*Self (Incongruent > Congruent) > Other (Incongruent > Congruent)*): (A) right middle occipital gyrus, (B) right precentral gyrus, (C) right putamen, (D) left putamen.

4.3 Behavioral Results Study 2

Table 11 displays the mean ratings and standard deviations for the 15 ASD participants compared with those of the 15 controls for both target sequences (DS and DO). As in Study 1, relevant inclusion and exclusion trials differ depending on the target of the rating. For the Double Self Sequence, IN/IN and IN/EX are inclusion trials, while EX/EX and EX/IN are exclusion trials. For Double Other, IN/IN and EX/IN are inclusion trials and EX/EX and IN/EX are exclusion trials (see section 4.1 for a more detailed explanation). A four-factorial (2 x 2 x 2 x 2) mixed ANOVA (GLM) was used to calculate the degree of empathic judgements. As in Study 1, all exclusion trials were multiplied by -1 prior to the analysis so that all trial means had a positive sign and were thus comparable. Once again, a significant main effect of congruency was found ($F_{(1,28)} = 25.620$, $p < .001$, $\eta_p^2 = 0.487$), revealing that there was a significant average difference between congruent and incongruent trials (congruent – incongruent: *M*/*SE* = 1.98/0.39; $p < .001$) with participants rating less extremely during incongruent trials (*M*/*SE* = 2.38/0.31) than congruent trials (*M*/*SE* = 4.36/0.46).

Table 11

Mean ratings and mean biases (as well as standard deviations) for both target sequences.

Target Sequence			ASD	Control
			M (SD)	M (SD)
DS	Trial (S/O)	IN/IN	2.94 (2.54)	5.48 (3.59)
		IN/EX	0.58 (2.41)	1.12 (2.61)
		EX/EX	-4.19 (3.97)	-4.87 (3.47)
		EX/IN	-2.03 (3.19)	-3.15 (3.66)
	Valence Bias	Inclusion Bias	2.15 (2.71)	1.73 (4.00)
		Exclusion Bias	2.37 (3.21)	.37 (4.36)
	Overall Bias	AB	2.26 (2.55)	3.05 (3.66)
DO	Trial (S/O)	IN/IN	3.24 (3.43)	4.20 (3.45)
		IN/EX	-2.93 (1.97)	-3.30 (4.14)
		EX/EX	-5.40 (3.25)	-4.59 (3.63)
		EX/IN	1.71 (2.61)	4.24 (3.54)
	Valence Bias	Inclusion Bias	2.47 (2.24)	1.29 (3.91)
		Exclusion Bias	1.53 (3.77)	0.04 (2.20)
	Overall Bias	EEB	2.00 (2.50)	0.64 (2.32)

Note. To calculate the biases, the absolute values of the trial means were used. The Exclusion Bias was calculated by subtracting IN/EX from IN/IN (for DS) and EX/IN from IN/IN (for DO). The Inclusion Bias was calculated by subtracting EX/IN from EX/EX (for DS) and IN/EX from EX/EX (for DO). The Overall Bias was calculated as the mean of the Inclusion and Exclusion biases. ASD = Autism Spectrum Disorder; DS = Double self; DO = double other; S = Self; O = Other; IN = Inclusion; EX = Exclusion; AB = Altercentric Bias, EEB = Emotional Egocentricity Bias.

This means that, like in Study 1, participants' ratings were drawn towards the emotional state of the person not currently being rated during incongruent trials. Figure 9 shows the un-inverted mean ratings for both groups in the DO and the DS condition, while Figure 10 depicts the overall AB and EEB for the entire sample as well as separately for the two groups.

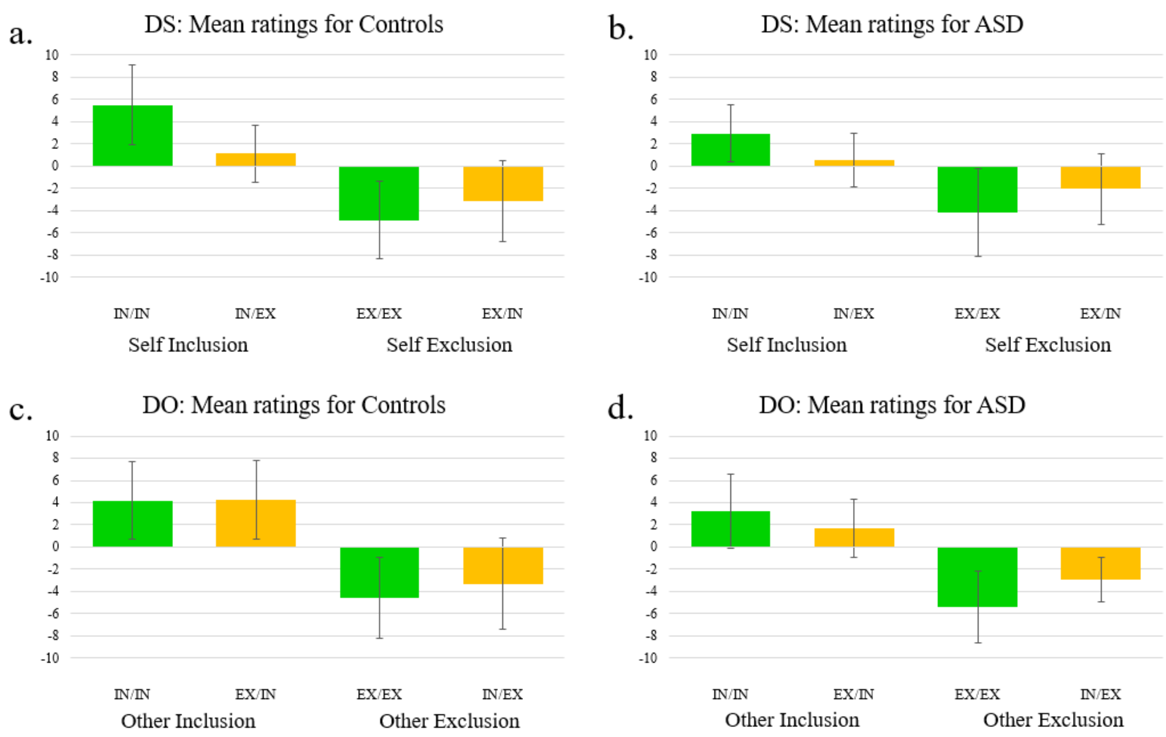

Figure 9. Plotted un-inverted mean rating values and standard deviations for (a) the Control group in the DS condition (b) the ASD group in the DS Condition (c) the Control group in the DS condition and (d) the ASD group in the DO condition. Mean ratings are separated by valence (Inclusion and Exclusion). Congruent trials are shown in green, incongruent trials in orange. ASD = Autism Spectrum Disorder; DS = Double Self; DO = Double Other.

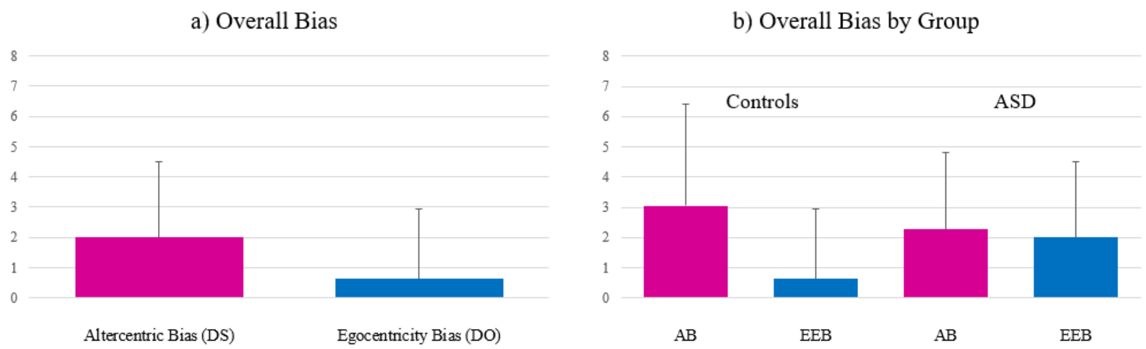

Figure 10. Plot of overall values of the Altercentric Bias and the Egocentricity Bias for (a) the whole sample and (b) separated by group (ASD versus Controls). To calculate the overall bias for each condition, incongruent trials were subtracted from congruent trials. DS = Double Self; DO = Double Other, AB = Altercentric Bias, EB = Egocentricity Bias.

Additionally, there was a significant three-way interaction for target x valence x congruency ($F_{(1,28)} = 12.466$, $p = .001$, $\eta_p^2 = 0.308$). Planned comparisons via simple effects analysis showed that in the DS condition, there were significant differences between congruent and incongruent trials both when the self was included (congruent – incongruent = 3.367, $SE = 0.699$, $p < .001$) and when the self was excluded (congruent – incongruent = 1.941, $SE = 0.624$, $p = .004$). However, in the DO condition there was no significant difference between congruent and incongruent trials when the other was included (congruent – incongruent = 0.747, $SE = 0.564$, $p = .196$) compared to when the other was excluded (congruent – incongruent = 1.880, *SE* = 0.582, $p = .003$). In other words, the average rating of emotional intensity was always higher in the congruent trials than in the incongruent trials which is to be expected, since the rating was always biased in the opposite direction in incongruent trials, however, this difference was not significant for exclusion trials in the DO condition. This was true for all participants, as no influence of the group factor could be found.

No other main effects or interactions were significant (target, $F_{(1,28)} = 3.831$, $p = .060$, $\eta_p^2 = 0.120$; valence, $F_{(1,28)} = 2.051$, $p = .163$, $\eta_p^2 = 0.068$; target x group, $F_{(1,28)} = 0.466$, $p = .501$, $\eta_p^2 = 0.016$; valence x group, $F_{(1,28)} = 1.156$, $p = .291$, $\eta_p^2 = 0.040$; congruency x group, $F_{(1,28)} = 0.138$, $p = .713$, $\eta_p^2 = 0.005$; target x valence, $F_{(1,28)} = 0.266$, $p = .610$, $\eta_p^2 = 0.009$; target x valence x group, $F_{(1,28)} = 1.1222$, $p = .299$, $\eta_p^2 = 0.039$; target x congruency, $F_{(1,28)} = 4.122$, $p = .052$, $\eta_p^2 = 0.128$; target x congruency x group, $F_{(1,28)} = 2.667$, $p = .114$, $\eta_p^2 = 0.087$; valence x congruency, $F_{(1,28)} = 0.061$, $p = .806$, $\eta_p^2 = 0.002$; valence x congruency x group, $F_{(1,28)} = 0.730$, $p = .400$, $\eta_p^2 = 0.025$; target x valence x congruency x group, $F_{(1,28)} =3.797$, $p = .061$, $\eta_p^2 = 0.119$). To analyze whether there was an overall size difference between the EEB and the AB, a paired sample *t*-Test was calculated. The results showed no significant difference between the EEB and the AB: $t(29) = 1.974$, p = .058, with the EEB (*M/SE*) = 1.31/0.45 and the AB (*M/SE*) = 2.65/0.45). To investigate the association between the mean AB, EEB and individual levels of alexithymia, trait empathy and autistic traits, two-sided Spearman correlations were calculated. There as significant negative correlation between the EEB and the *Perspective Taking* scale of the empathy questionnaire ($r_s = -.383$, $p = .036$). Furthermore, the measure for autistic traits showed significant negative correlations with two subscales of the empathy questionnaire (*Fantasy*: $r_s = -.421$, $p = .020$; *Perspective Taking*: $r_s = -.599$, $p < .001$) and significant positive correlations with all scales of the alexithymia questionnaire (*Difficulty Identifying Feelings*: $r_s = .647$, $p < .001$; *Difficulty Describing Feelings*: $r_s = .626$, $p < .001$; *Externally Oriented Thinking*: $r_s = .459$, $p = .011$). All correlations can be found in Table A2 in the supplementary material.

4.4 Neuroimaging Results Study 2

Sample size for the fMRI analysis of Study 2 consisted of 15 adult male participants with ASD and 15 adult male neurotypical control participants. Only the main effects will be reported here, as no significant clusters were found for any two- or three-way interactions.

Main effect of experiment. The main effect of experiment shows the overall effect playing the game had on all participants (ASD and controls) compared to a baseline. A whole brain contrast revealed enhanced hemodynamic activity in the following regions: bilateral calcarine cortex, left middle occipital gyrus, and right middle temporal gyrus (see Table 12).

Table 12
Main effect of experiment (Game > Baseline)

						Coordinates [mm]		
H	Anatomical Region	Cluster K	*p* (unc)	*T*	Z score	x	y	z
L	Calcarine cortex	2337	< .001	14,62	Inf	-6	-92	10
R	Calcarine cortex		< .001	12,48	Inf	10	-90	12
L	Calcarine cortex		< .001	5,32	5,16	-12	-76	-8
L	Middle occipital gyrus	973	< .001	14,51	Inf	-46	-74	4
R	Middle temporal Gyrus	1318	< .001	14,44	Inf	48	-62	4
R	Middle temporal Gyrus		< .001	14,12	Inf	50	-70	2
R	Fusiform gyrus	17	< .001	3,81	3,74	42	-40	-16

Note. H = Hemisphere, R = Right hemisphere, L = Left hemisphere.

Main effect of group. Compared to the control group, autistic participants showed overall higher activation in the following anatomical regions: left middle occipital gyrus, bilateral lingual gyrus, bilateral calcarine cortex, left superior occipital gyrus, left hemispheric lobule VI, right cuneus cortex, and right inferior temporal gyrus (see Table 13 and Figure 11). In contrast, no significant regions of increased activation could be found for control participants when compared to the ASD group (p = .001).

Table 13
Main effect of group (ASD > Control)

						Coordinates [mm]		
H	Anatomical Region	Cluster K	*p* (unc)	*T*	Z score	x	y	z
L	Middle occipital gyrus	189	<.001	4.72	4.60	-38	-72	0
R	Lingual gyrus	668	<.001	4.46	4.36	20	-66	-6
L	Lingual gyrus	11	<.001	3.39	3.35	-16	-46	0
R	Calcarine cortex		<.001	4.34	4.25	20	-54	8

(continued)

H	Anatomical Region	Cluster K	*p* (unc)	*T*	Z score	Coordinates [mm] x	y	z
R	Calcarine cortex		<.001	3.98	3.90	6	-92	4
L	Calcarine cortex	265	<.001	4.14	4.06	-20	-60	8
L	Calcarine cortex		<.001	3.99	3.91	-14	-64	18
L	Calcarine cortex	155	<.001	4.10	4.03	-4	-94	6
L	Superior occipital gyrus	34	<.001	4.18	4.09	-14	-86	30
L	Hemispheric lobule VI	49	<.001	4.04	3.97	-16	-58	-14
R	Cuneus cortex	59	<.001	3.73	3.67	20	-88	14
R	Inferior temporal gyrus	11	<.001	3.42	3.38	50	-52	-4

Note. H = Hemisphere, R = Right hemisphere, L = Left hemisphere.

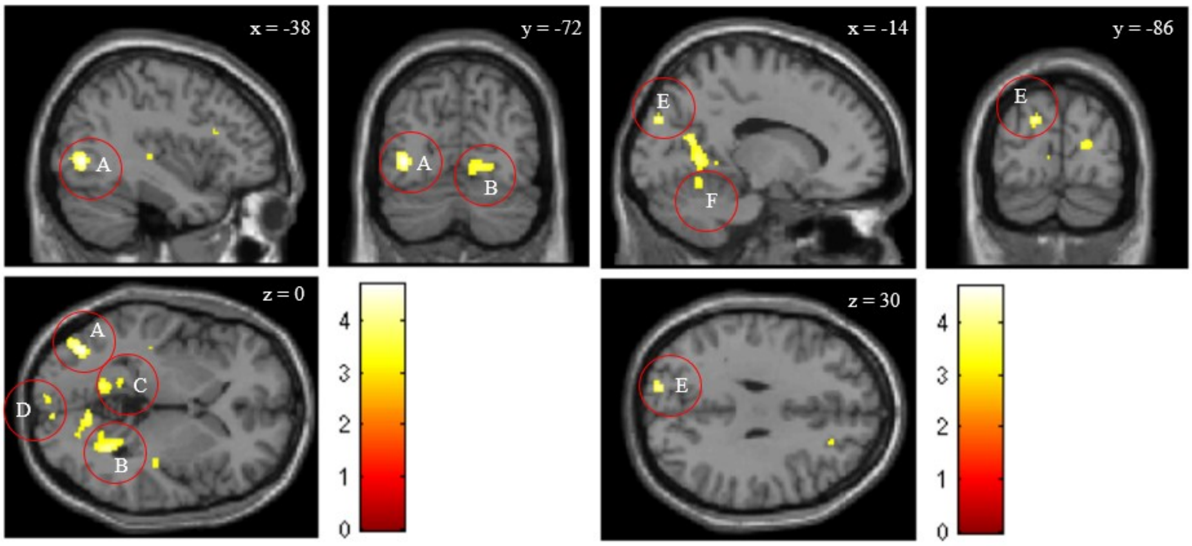

Figure 11. Regions of enhanced activation for the main effect of group *(ASD > Control)*: (A) left middle occipital gyrus, (B) right lingual gyrus, (C) left lingual gyrus, (D) bilateral calcarine cortex, (E) left superior occipital gyrus, and (F) left hemispheric lobule VI.

Main effect of target. No supra-threshold clusters could be detected for the main effect of target. Neither in the Self condition (when compared to the Other condition) nor in the Other Condition (when compared to the Self condition) could any increased activation be detected (p = .001).

Main effect of valence. During inclusion trials, participants showed increased activation in the following regions (as compared to exclusion trials): right superior temporal gyrus, right superior occipital gyrus, bilateral insula, left dorsolateral superior frontal gyrus, bilateral median cingulate gyrus, left supplementary motor area, bilateral precuneus cortex, right precentral gyrus, right inferior frontal cortex (opercular part), bilateral fusiform gyrus, bilateral middle temporal gyrus, left postcentral gyrus, left hemispheric lobule VI, and left cerebellum (see Table 14).

Table 14

Main effect of valence (Inclusion > Exclusion)

						Coordinates [mm]		
H	Anatomical Region	Cluster K	*p* (unc)	*T*	Z score	x	y	z
R	Superior temporal gyrus	3257	<.001	5.46	5.28	54	-48	18
R	Superior temporal gyrus		<.001	5.40	5.23	62	-44	20
R	Superior occipital gyrus		<.001	4.42	4.32	24	-68	30
R	Insula	259	<.001	4.89	4.76	32	24	8
L	Insula	82	<.001	3.99	3.92	-32	20	10
L	Dorsolateral superior frontal gyrus	202	<.001	4.77	4.65	-24	0	48
R	Median cingulate gyrus	49	<.001	3.73	3.67	12	14	46
L	Median cingulate gyrus	234	<.001	4.53	4.42	-10	14	44
L	Supplementary motor area		<.001	4.19	4.10	-10	2	56
R	Precuneus cortex	184	<.001	4.37	4.27	10	-50	48
R	Precuneus cortex		<.001	3.89	3.82	8	-58	48
L	Precuneus cortex	19	<.001	3.49	3.44	-10	-52	48
L	Precuneus cortex	22	.001	3.32	3.28	-12	-64	50
L	Precuneus cortex	24	<.001	3.47	3.42	-16	-70	36
R	Precentral gyrus	144	<.001	3.77	3.71	34	4	48
R	Inferior frontal gyrus, opercular part	30	<.001	3.65	3.59	50	10	14

(continued)

H	Anatomical Region	Cluster K	*p* (unc)	*T*	Z score	Coordinates [mm] x	y	z
R	Fusiform gyrus	40	<.001	3.55	3.50	38	-42	-14
L	Fusiform gyrus	48	<.001	3.48	3.43	-28	-58	-10
R	Middle Temporal Gyrus		.001	3.30	3.26	48	-44	-12
L	Middle Temporal Gyrus		<.001	3.40	3.35	-52	-46	12
L	Postcentral gyrus	35	<.001	3.50	3.45	-34	-22	48
L	Hemispheric lobule VI	16	<.001	3.35	3.30	-30	-56	-32
L	Cerebellum		.001	3.30	3.26	-38	-56	-34

Note. H = Hemisphere, R = Right hemisphere, L = Left hemisphere.

During exclusion trials, participants showed a greater hemodynamic response in the following regions (as compared to inclusion trials): right precentral gyrus, right postcentral gyrus, left paracentral lobule, left medial superior frontal gyrus, left inferior frontal gyrus (triangular part), left temporal pole (superior temporal gyrus), right supplementary motor area, left calcarine cortex, and vermic lobule III (see Table 15).

Table 15
Main effect of valence (Exclusion > Inclusion)

H	Anatomical Region	Cluster K	*p* (unc)	*T*	*Z* score	Coordinates [mm] x	y	z
R	Precentral gyrus	1022	<.001	6.26	6.00	20	-22	68
R	Postcentral gyrus		<.001	3.68	3.62	50	-14	54
L	Paracentral lobule	450	<.001	5.51	5.33	-18	-26	66
L	Paracentral lobule		<.001	3.63	3.58	0	-28	54
L	Medial superior frontal gyrus	2020	<.001	5.49	5.31	-8	30	62
L	Medial superior frontal gyrus		<.001	5.29	5.13	-2	48	44
L	Medial superior frontal gyrus		<.001	5.00	4.86	-10	50	44
L	Inferior frontal gyrus, triangular part	133	<.001	4.19	4.11	-58	26	20

(continued)

						Coordinates [mm]		
H	Anatomical Region	Cluster K	*p* (unc)	*T*	*Z* score	x	y	z
L	Temporal pole, superior temporal gyrus	70	<.001	3.98	3.91	-42	10	-18
R	Supplementary motor area	145	<.001	3.88	3.82	0	-14	66
L	Calcarine cortex	68	<.001	3.66	3.60	-8	-90	-6
	Vermic lobule III	10	<.001	3.48	3.43	0	-42	-12

Note. H = Hemisphere, R = Right hemisphere, L = Left hemisphere.

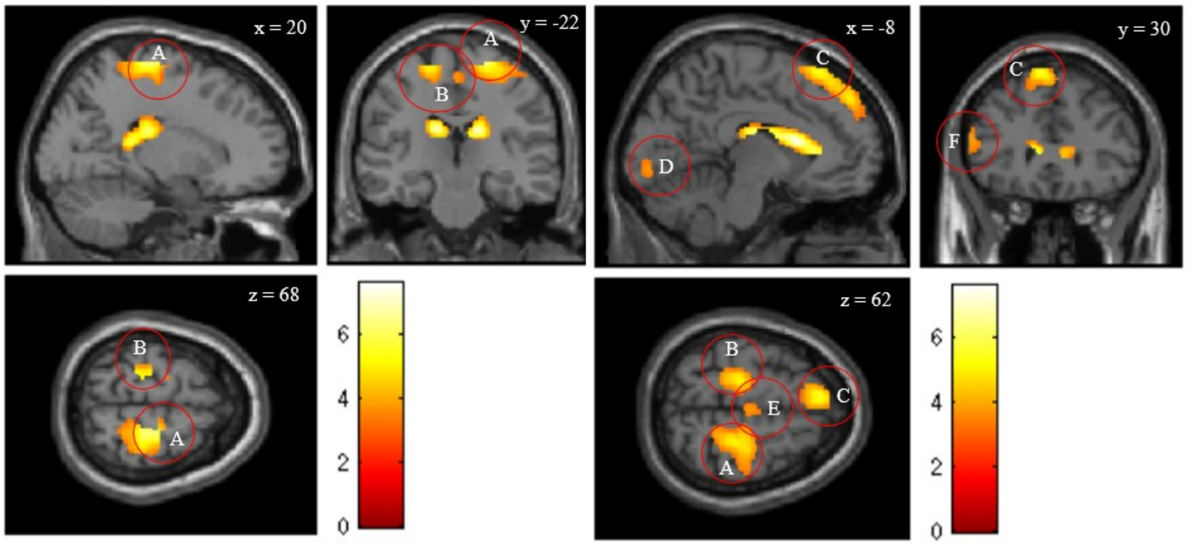

Figure 12. Regions of enhanced activation for the main effect of valence *(Exclusion > Inclusion)*: (A) right precentral gyrus, (B) left paracentral lobule, (C) left medial superior frontal gyrus, (D) left calcarine cortex, (E) right supplementary motor area and (F) left inferior frontal gyrus.

Main effect of congruency. The main effect of congruency describes the difference in neural activity between congruent and incongruent trials (i.e. when a bias appears). During congruent trials, a significant increase in activation could be found in the right calcarine cortex only (see Table 16). However, during incongruent trials, there was increased activation in the following regions: left medial superior frontal gyrus, right middle temporal gyrus, left caudate nucleus, bilateral precuneus cortex, left inferior occipital gyrus, right cuneus cortex, bilateral superior parietal gyrus, left inferior parietal gyrus, bilateral middle frontal gyrus, bilateral inferior frontal gyrus (triangular part), right lingual gyrus, bilateral superior occipital gyrus, left thalamus, right cerebellum, left posterior cingulate gyrus and left angular gyrus (see Table 17).

Table 16

Main effect of congruency (Congruent > Incongruent)

						Coordinates [mm]		
H	Anatomical Region	Cluster K	*p* (unc)	*T*	*Z* score	x	y	z
R	Calcarine cortex	36	<.001	3,41	3,36	20	-52	6

Note. H = Hemisphere, R = Right hemisphere, L = Left hemisphere.

Table 17

Main effect of congruency (Incongruent > Congruent)

						Coordinates [mm]		
H	Anatomical Region	Cluster K	P (unc)	T	Z score	x	y	z
L	Medial superior frontal gyrus	4183	<.001	6.08	5.85	-4	30	62
L	Medial superior frontal gyrus		<.001	5.48	5.30	-2	44	46
L	Medial superior frontal gyrus		<.001	4.77	4.65	0	54	34
R	Middle temporal gyrus	1419	<.001	5.43	5.25	50	-64	4
L	Middle temporal gyrus		<.001	4.57	4.46	-44	-64	8
L	Caudate nucleus	833	<.001	4.94	4.81	-8	14	14
R	Precuneus cortex	823	<.001	4.87	4.74	6	-46	52
R	Precuneus cortex		<.001	3.52	3.46	10	-64	66
R	Precuneus cortex	136	<.001	3.66	3.60	2	-54	28
L	Precuneus cortex		<.001	3.59	3.54	-16	-62	66
L	Precuneus cortex		<.001	4.27	4.18	-6	-44	56
L	Inferior occipital gyrus	1797	<.001	4.82	4.69	-44	-80	-2
R	Cuneus cortex		<.001	4.24	4.16	6	-80	-20
R	Cuneus cortex	25	<.001	3.43	3.38	12	-98	8
R	Superior parietal gyrus	262	<.001	4.27	4.18	24	-56	60
R	Superior parietal gyrus		<.001	3.86	3.79	24	-48	62
L	Superior parietal gyrus	488	<.001	4.17	4.09	-26	-52	60

(continued)

						Coordinates [mm]		
H	Anatomical Region	Cluster K	P (unc)	T	Z score	X	y	z
L	Inferior parietal gyrus		<.001	3.38	3.34	-42	-48	58
R	Middle frontal gyrus	416	<.001	4.16	4.08	52	14	46
R	Middle frontal gyrus		<.001	3.49	3.44	36	10	38
R	Middle frontal gyrus		<.001	3.44	3.39	50	26	40
L	Middle frontal gyrus		<.001	3.68	3.62	-38	54	4
R	Inferior frontal gyrus, triangular part	58	<.001	3.89	3.82	58	22	26
R	Inferior frontal gyrus, triangular part	11	<.001	3.34	3.30	38	22	24
L	Inferior frontal gyrus, triangular part	87	<.001	3.74	3.68	-42	42	0
R	Lingual gyrus	10	<.001	3.77	3.71	14	-92	-12
R	Superior occipital gyrus	59	<.001	3.73	3.67	16	-90	24
L	Superior occipital gyrus	42	<.001	3.69	3.63	-8	-98	-10
L	Thalamus	28	<.001	3.72	3.66	-14	-24	18
L	Thalamus		<.001	3.53	3.47	-10	-16	20
R	Cerebellum	22	<.001	3.72	3.66	30	-82	-20
L	Posterior cingulate gyrus		0.001	3.32	3.27	-6	-50	34
L	Angular gyrus	74	<.001	3.63	3.57	-44	-64	34

Note. H = Hemisphere, R = Right hemisphere, L = Left hemisphere.

5 Discussion

The aim of this study was to provide a valuable addition to the vast range of already existing empathy literature in the field of social cognitive neuroscience. Empathy is a complicated socio-cognitive phenomenon, and to get a better understanding of it, one should examine it carefully while considering the various related concepts and components that play a part in reproducing and feeling others emotions (Walter, 2012). Recent research has established that empathy can be essentially divided into two interacting components: affective empathy, the process which allows us to feel another person's affective state through emotional contagion, and cognitive empathy, which encompasses such processes as mentalizing, self-other distinction and perspective taking (Batson, 2009; Dziobek et al., 2008; Shamay-Tsoory et al., 2009). Self-other distinction is a crucial aspect of empathy without which we would not be able to differentiate between our own and other people's feelings. Even though we generally use our own affective state as an anchor to judge other's emotions (Hoffmann et al., 2016a; Lamm et al., 2016), SOD allows us to make informed inferences about what another person might actually be thinking or feeling and helps to avoid feelings of confusion and even personal distress, which could happen if emotional contagion went unchecked without top-down cognitive influence to regulate it (Singer & Lamm, 2009). However, like all cognitive processes, self-other distinction and empathy in general are not perfect, and a deficit in SOD can lead to biased judgments in one of two ways: Firstly, when asked to empathically assess the feelings of another person, we can become overly influenced by our emotions and thus show a bias toward our own affective state (i.e. Emotional Egocentricity Bias). Secondly, when it comes to gauging our own feelings, we are sometimes so impacted by another person's emotions that it distorts our rating in that direction, which has been called Altercentric Bias (Hoffmann et al., 2016a; Silani et al., 2013). Furthermore, studies investigating the pathology of empathy have found that certain aspects of cognitive empathy, including self-other distinction, may be disrupted in Autism Spectrum Disorder (Lockwood, 2016; Preston & de Waal, 2002; Schulte-Rüther et al., 2014), which makes ASD a particularly crucial research topic in this domain. In this thesis, I therefore sought to investigate the presence of the EEB as well as the AB and their underlying neural mechanisms in both a neurotypical population as well as participants with ASD. To that end, both behavioral and neuroimaging data was collected over the course of two studies, using a version of the well-established Cyberball paradigm (Novembre et al., 2015; Williams et al., 2000). This interactive virtual ball-tossing game represents a social group interaction in which situations of both inclusion and exclusion can be artificially generated to invoke positive and negative feeling states. By putting the participants in incongruent and congruent affective states with another player and then asking them to rate either their own feelings or those of the other person, the EEB and AB can be calculated.

I had hypothesized that both adult neurotypical participants as well as people with ASD would display some degree of an EEB as well as an AB. Furthermore, with the EEB being the more robust and better documented phenomenon, I predicted that the EEB would be larger than the AB and that the autistic participants would show significantly higher biases than the control group. Finally, I anticipated that the biases would be accompanied by increased hemodynamic activity in the right supramarginal gyrus (rSMG) and the right temporoparietal junction (rTPJ), both being brain regions directly associated with self-other distinction (Decety & Lamm, 2007; Lamm et al., 2016; Silani et al., 2013).

The behavioral results from Study 1 showed that, as hypothesized, neurotypical adults exhibited both an EEB and an AB when they were in incongruent affective states to the person opposite them. This was irrespective of whether the person currently not being rated (i.e. the person in whose direction that rating was skewed) was being excluded or included, as the participants showed both an Inclusion Bias and an Exclusion Bias. The existence of both biases was confirmed via the repeated measures ANOVA, which found the main effect of congruency to be significant. These results are in line with those from previous studies on the Emotional Egocentricity Bias in the general population (Riva, Triscoli, Lamm, Carnaghi, & Silani, 2016; Silani et al., 2013; Steinbeis et al., 2014) and, more excitingly, corroborate the results from Hoffmann et al. (2016a), one of the only recent studies to investigate the Altercentric bias. While Hoffmann et al. studied a clinical sample (namely patients with MDD), the results from this study suggest that like the EEB, the AB is not only present in people with empathy disorders, but also in the general population and that like people with ASD, neurotypical participants struggle with self-other distinction when they are in a situation where another person feels markedly different than they do. Interestingly, the ANOVA showed no other significant results. The absence of an interaction effect of valence and congruency indicated that there was no difference in size between the inclusion and the exclusion biases for either condition, meaning that whether the person being rated was in a positive or negative affective state had no influence on the size of the bias. While I had not formulated any specific hypothesis regarding this effect, it is still somewhat surprising, since past research has shown that negative stimuli often result in stronger emotional reactions than positive ones (Bernhardt & Singer, 2012; de Vignemont & Singer, 2006; Preston & Hofelich, 2012). So, it would not have been surprising if the exclusion bias had been larger than the inclusion bias. Furthermore, the absence of an interaction effect between congruency and target shows that there was no significant difference in size between the EEB and the AB, contrary to what I had hypothesized, although this interaction had come close to significance. Interestingly, however, even though not significant, the trend in the data showed the opposite to the original prediction, with the AB being larger than the EEB. While surprising at first, this could be explained by the fact that this paradigm might not have measured an AB at all, but rather a form of empathy, and that in their rating, participants were actively considering what the other person felt and how they themselves were affected by it. This will be discussed in greater detail further down. Finally, a correlation between the biases and self-report data on both trait empathy and alexithymia showed no significant association between the scales and either the EEB or the AB. A significant correlation between the scores on the *Perspective Taking* scale of the empathy questionnaire and autistic traits was not surprising, as the impairments in perspective taking are a core diagnostic component of Autism Spectrum Disorder and are thus part of what is being assessed by the ASD questionnaire.

Behavioral data for Study 2 revealed, once again, a main effect of congruency, replicating results from Study 1 and substantiating the hypothesis that there would also be an EEB and an AB in this sample. Additionally, a three-way interaction effect between the conditions target, valence and congruency was found, revealing that the difference in ratings between the congruent and incongruent trials was not significant in one specific situation, namely during exclusion trials in the DO condition. That is to say, when participants were asked to rate the person opposite them while that person was being excluded, the raters did not display a significant shift in rating towards their own feelings. It is unclear why the effect of the EEB should appear in all conditions except this one. However, as mentioned before, situations of negative emotional valence often have a much higher salience than positive ones (Bernhardt & Singer, 2012; de Vignemont & Singer, 2006). Additionally, while neither a main effect of target nor an interaction effect of target and valence could be found, many participants reported during the final debriefing that they had felt stronger feelings of social injustice when the other person was being excluded than when they themselves were being excluded. Thus, exclusion for the other person could have been such a salient anchor, that only very little rating bias was taking place, and this might have only been the case for the other condition, because participants simply did not care as much if they themselves were being excluded.

Unfortunately, there were no significant main or interaction effects involving the factor group, meaning that no difference in ratings could be found between ASD participants and controls. The hypothesis that people with ASD would display higher biases could therefore not be confirmed. This is surprising, as there is much evidence that people with Autism Spectrum Disorder have deficits in cognitive empathy (see Baird, Scheffer, & Wilson, 2011 and Frith & Happé, 2005, for reviews). It is possible that this effect was mitigated by the fact all the autistic participants in this study were high-functioning adults and had developed compensatory mechanisms for a lack of spontaneous ToM over their lifetime, as has been previously found (Schulte-Rüther et al., 2014; Sebastian et al., 2012). Additionally, the Cyberball game for this study had been specifically designed for the use of people with ASD, minimizing any distracting elements such as facial expressions in the avatars. This might have aided the ASD participants to employ self-other distinction as effectively as the control group. Finally, it is important to keep in mind that sample size for Study 2 was rather small, and a bigger sample may have shown significance effects and led to clarity on this issue. Finally, I found a significant negative correlation between the overall EEB and the *Perspective Taking* subscale of the self-report empathy questionnaire, which indicates that people who show a higher EEB seem to be somewhat aware of this fact, as they report having difficulties assuming the cognitive perspective of another person.

Disappointingly, the neuroimaging data for both studies showed little overall activation and no activation in the regions that had been predicted beforehand (i.e. rTPJ and rSMG). When compared to a baseline of no activation, the main effect of the game for both Study 1 and Study 2 showed an increase in activation in regions generally associated with visual motion perception and face processing (Grossman & Blake, 2002; Preston & de Waal, 2002). This was to be expected, as participants were watching video clips of moving human avatars.

For Study 1, the main effect of target showed no regions of increased activation when participants were asked to rate the other person in comparison to being asked to rate themselves. Conversely, there were only two significant clusters of enhanced hemodynamic activity during the self-rating condition as compared to the other-rating condition: the right superior temporal pole (rSTP) and right putamen. Although the temporal poles have sometimes been indicated in mentalizing processes (Mar, 2011), the putamen is generally linked to motor control and learning (Jueptner & Weiller, 1998). The activation of the temporal poles in this case is also puzzling, as participants should not have had to employ Theory of Mind while they were rating their own feelings, though it is of course possible that they were in fact actively thinking about the other person's feelings and trying to take them into account while they were judging their own emotional state, as I mentioned above. For the main effect of valence, comparing inclusion to exclusion trials revealed increased hemodynamic activity in regions associated with working memory and language decoding (Boisgueheneuc et al., 2006; Hoffman, Pobric, Drakesmith, & Ralph, 2012), but also areas associated with the limbic system and emotion processing (Lamm et al., 2011; Singer, 2006). While this seems difficult to interpret because working memory (and language decoding as well) should not be more relevant in one condition than the other, comparing exclusion to inclusion on the other hand and revealed more clear results: the highest activation occurred in the postcentral and precentral gyri, both of which have been indicated in the affective components of pain perception in self and others (Bernhardt & Singer, 2012; Ochsner et al., 2008). As the exclusion trials were conceived to elicit negative feelings through social pain, while the inclusion trials should lead to positive or at least neutral feelings, this result was as expected and can also be seen as an indication that the paradigm's manipulation had an effect.

The main effect of congruency once again revealed very few areas of activation. During congruent trials (as compared to incongruent trials) the only clusters of enhanced hemodynamic activity were found in the lingual gyrus, which is part of the visual cortex and has been indicated in color processing (Zeki et al., 1991). This is difficult to interpret, as once again, there is little reason that visual processing should differ much between the incongruent and congruent trials. Contrasting incongruent with congruent trials showed an increase in activation in the middle temporal gyrus, which plays a role in semantic memory (Hoffman et al., 2012), but also the superior temporal gyrus and the precuneus which have been indicated as parts of the ToM-network (Mar, 2011; Singer, 2006). On one hand, this is in line with my hypotheses, indicating that participants had to make more use of their mentalizing skills during incongruent trials (i.e. where one must differentiate between one's own feelings and those of another person). On the other hand, counter to what had been postulated, there was no activation of the rTPJ or the rSMG, which, according to the a-priori hypothesis, would show increased activation during self-other distinction. In fact, neither the rSMG nor the rTPJ appeared as clusters of enhanced activation in any on the contrasts either in Study 1 or in Study 2. This is surprising, as there is solid evidence for the involvement of the rSMG during self-other distinction and the role of the rTPJ in empathy has been especially well documented (Lamm et al., 2016). Finally, the interaction effect of target and congruency, a contrast which essentially examines the differences between the two biases, showed some areas of increased activation when comparing the differences between incongruent and congruent trials while rating another person (i.e. the EEB) to the difference between incongruent and congruent while rating one's own feelings (i.e. the AB). Once again, a very heterogenous group of areas seemed to show increased hemodynamic activity, namely regions involved in pain processing, motor control and motor theory of empathy as well as regions associated with visual processing (Grossman & Blake, 2002; Jackson et al., 2005; Jueptner & Weiller, 1998; Leslie et al., 2004).

For Study 2, the main effect of group examined the overall difference in neural activation between the group of ASD participants the control group. Compared to the controls, autistic participants showed higher activation in the bilateral lingual gyrus and bilateral calcarine cortex, the superior occipital gyrus and the inferior occipital gyrus, all areas which are linked to visual processing (Fink et al., 1996; Grossman & Blake, 2002; Zeki et al., 1991). While it has been argued before that people with ASD may employ different brain areas when it comes to visual processing, especially for stimuli in the social domain such as facial cues, (Dapretto et al., 2006; Mazza et al., 2014), again, it seems unintuitive that this would be the only difference in activation. In fact, following Smith's (2009) empathy imbalance hypothesis of autism which postulates that individuals with ASD display a surfeit of affective empathy, one would expect an increase in activation in areas associated with social pain and emotional contagion. Additionally, there were no significant clusters of enhanced neural activity in the control group compared to the ASD group. Though this is contrary to my hypothesis which expected control participants to show more self-other distinction and thus more activity in the rSMG, it is in line with the behavioral results, which did not find a size difference in the biases between the two groups. Furthermore, no supra-threshold clusters could be detected for the main effect of target, indicating that there was seemingly no difference in neural activation between rating one's own feelings and rating those of another person.

A more meaningful number of clusters was activated for the main effect of valence. During inclusion trials (i.e. a positive or neutral emotional state), participants showed increased blood flow in areas associated with empathy, pain perception, visual motor perception, face processing and mentalizing (Bernhardt & Singer, 2012; Grossman & Blake, 2002; Leslie et al., 2004; Mar, 2011; Ochsner et al., 2008; Singer, 2006; Vogt, 2005). Conversely, during exclusion trials (i.e. in a negative affective state), participants showed enhanced activation in regions associated with the sensory motor network, namely the right precentral gyrus and the left paracentral lobule, the postcentral gyrus (sometime also associated with pain processing), the left paracentral lobule as well as the right supplementary motor area (Amiez & Petrides, 2014; Lamm et al., 2007; Philip et al., 2012). Additionally, enhanced activations were found for the left medial superior frontal gyrus (part of the dmPFC) which has been associated with higher cognitive functions like working memory and spatial cognition, the left calcarine cortex, the left temporal pole, which has been linked to processing of emotional stimuli and face processing as well as mentalizing, and finally the vermic lobule III which has been indicated in pain perception (Boisgueheneuc et al., 2006; Grossman & Blake, 2002; Mar, 2011; Singer, 2006). Once again, these results are mixed. While activation of areas associated with pain processing was expected during exclusion trials, this should not have been the case for the inclusion trials. Face processing, mentalizing and visual motor perception should not be increased in one condition over the other.

Finally, the main effect of congruency describes the differences in activation between congruent and incongruent trials. Only one small significant cluster of increased activation was found for the congruent trials (in comparison to the incongruent once), located in the right calcarine cortex, which is associated with visual processing, as mentioned above. Increased activations during incongruent trials was found in areas relating to Theory of Mind such as the bilateral precuneus cortex (Mar, 2011; Singer, 2006) but also affective empathy (the inferior frontal gyrus, Shamay-Tsoory et al., 2009) and pain processing (thalamus and cerebellum, Jackson et al., 2005). Additionally, activations were found in regions linked to visual processing such as the inferior and superior occipital gyrus and the lingual gyrus (Fink et al., 1996; Grossman & Blake, 2002; Zeki et al., 1991). There was also a small cluster of activation in the left angular gyrus, which is of interest because it encompasses the temporoparietal junction together with the supramarginal gyrus, however, activation of the angular gyrus was only found in the left hemisphere, while the areas of interest (rSMG, rTPJ) are located in the right (Silani et al., 2013).

To summarize, while some of the contrasts from both studies revealed areas of increased hemodynamic response that do in fact correspond to cognitive and affective processes that associated with empathy and social pain, the overall neuroimaging results were too heterogeneous to be interpreted effectively. It is possible that this is due to the specific approach that was taken during functional data acquisition and analysis. Firstly, it is possible that the high-pass filter for the elimination of noise was chosen too conservatively and thus filtered out relevant signal. Secondly, if a participant moves too much during scanning, it can distort the data. While subjects with excessive movement were generally excluded from the fMRI analysis, some ASD participants whose movement parameters came close to the critical threshold were kept in the sample to not further decrease the already small sample size. Thirdly, while a design modelling individual blocks of the game was chosen for data analysis, it is possible that an event-related design focusing on specific moments during the game (e.g. the exact point when a person is getting excluded) might be able to better differentiate between the different conditions. However, this may require some changes to the paradigm. In any case, it would be prudent to implement these changes in future studies.

Aside from the data analysis, this study has a few other limitations that should be addressed. Firstly, while we aimed to investigate both the Emotional Egocentricity Bias and the Altercentric Bias, it is possible that the participants really showed true empathy rather than a bias. For example, in incongruent trials of the Double Other condition, when participants were asked to rate the person opposite them, their ratings displayed a shift towards their own feeling state. The argument could be made however, that this was not an unconscious bias, but that the participants were actually employing second order Theory of Mind, assuming that the other person would also be influenced by their own feelings (e.g. "The other person is currently being included, so they should be happy. However, they know that I am currently being excluded, and they probably feel empathic towards me, so they are not as happy as they would be if we were both being included."). This possible weakness in the paradigm was actually taken into account for this experiment and addressed through a separate control condition (*Double Other passive*) and the actual comparison between the DOa and DOp conditions was the subject of a different thesis (for results, see Hartmann, 2017). However, a similar problem could arise for the Self condition. While the results show that subjects' judgements of their own emotions were indeed influenced by the other person's affective state, it is not clear that this was happening through pure emotional contagion, since the participants were only asked "How are you currently feeling?" and not "Why are you feeling this way?". Again, what could actually have been the case is that participants were employing both cognitive and affective empathy and were consciously integrating the knowledge about the other persons' state into their own ratings (e.g. "I am being included, but the other person is being excluded. I would be happier if we were both being included."). Future studies investigating the AB should therefore attempt to create a control condition similar to the one for the EEB.

It should also be noted that participants were asked for feedback about the study during the final debriefing and were specifically questioned about whether they had believed the paradigm. This revealed that most subjects, irrespective of group, had noticed or at least suspected that they were playing against a computer at some point during the game, the reasons being that the paradigm felt too unrealistic and not like a real game (e.g. it was too repetitive and predictable). Some also mentioned that they felt it was unlikely that real people would suddenly start excluding other players for no reason. When asked whether they had felt any emotional involvement in the game, most participants admitted they had felt no or very little emotions, stating that they did not really care whether they were excluded or included in a ball game that had no consequences, and also that the artificial situation of lying in the scanner playing a virtual game was too far removed from real life to feel like a social situation. It is interesting, however, that the participants still rated as though they were feeling emotionally involved in the game. One reason for this might be that even though they did not admit it, participants still felt social pain during exclusion. As Zadro, Williams, and Richardson (2004) have shown, Cyberball can elicit negative feelings even when participants know they are playing against a computer. It is however also possible that the ratings were based on social desirability. All study participants were highly motivated, and as the paradigm is not overly difficult to understand, it is possible that people simply rated in a way they thought was expected of them. While this is a strong possibility, it does not explain the existence of an Emotional Egocentricity Bias in the data, so it seems like the participants did show emotional reactions, at least to some extent.

Finally, this study was limited by its small sample size, which was largely due to the challenges that are presented when recruiting subjects from a relatively small clinical population, especially since it was also necessary to exclude potential participants who did not meet the fMRI criteria. Additionally, the entire sample consisted largely of men. For Study 1, this was done to avoid gender as a confounding variable, as controlling for gender would have led to even smaller subgroups in an already small sample size. For Study 2, all subjects with ASD who volunteered and met the inclusion criteria were accepted, but due to the fact that autism is much more prevalent in men (Werling & Geschwind, 2013), only two women (matched with two female controls) were included. Therefore, the findings of this study cannot be readily generalized to the overall population. Future studies should aim to improve the Cyberball game for a believable and ecologically valid paradigm, while also including a control condition for the Altercentric Bias and aiming to better adjust the functional data analysis.

Nevertheless, the behavioral results from this study provide solid evidence for the existence of both egocentrically and altercentrically biased emotional judgements in healthy adults as well as in adults with Autism Spectrum Disorder. The fact that no difference in empathic skills could be found between the two groups indicates that, given the right conditions, people with Asperger's syndrome are capable of Theory of Mind and self-other distinction at a level similar to that of neurotypical adults. The results of this study also confirm that empathy is a complex socio-economic phenomenon depending on elaborately interconnected neural structures, which makes it so valuable to investigate these basic processes to gain a greater understanding on human interactions as a whole.

6 References

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7 Appendix

List of Tables

List of Figures

English Abstract

Empathy, the human ability to vicariously experience the affective states of other people, can generally be divided into two key components: *affective empathy* (the ability to feel others' emotions) and *cognitive empathy* (the ability to deduce the mental states of others). In the context of cognitive empathy, *self-other distinction* allows us to correctly differentiate between our own feelings or mental states and those of someone else, a crucial step without which true empathy would not be possible. This thesis aimed to study situations where self-other distinction can be impaired, which can lead to a bias in the judgement of both one's own as well as others' feelings, while investigating the underlying neuronal mechanism through functional magnetic resonance imaging (fMRI). Using a virtual ball game to create an interactive social situation, we induced positive and negative affective states in participants through systematic inclusion and exclusion. Participants then had to alternatively rate their own feelings and those of another player. This paradigm was used to investigate a sample of twenty neurotypical adult men (Study 1) as well as 15 adult participants with Autism Spectrum Disorder (ASD), matched with 15 control participants (Study 2). Results of Study 1 showed that in incongruent situations, namely when one person was included (i.e. in a positive affective state) but the other person was excluded (i.e. in a negative affective state), ratings shifted in the direction of the person not being rated. Thus, when participants were asked to rate themselves in incongruent situations, they were influenced by the other person's feelings, an effect called an *Altercentric Bias*. Conversely, when participants had to rate the other person, they were affected by their own emotional state, which is called *Emotional Egocentricity Bias*. Study 2 once again found the existence of the AB and the EEB, however, there were no differences between the two groups, indicating that people with ASD showed similar levels of self-other distinction and cognitive empathy as neurotypical participants. Neuroimaging results showed some activity in brain regions associated with both affective and cognitive empathy during incongruent trials, but were generally inconclusive. Results from previous studies, which indicated strong activation of both the right supramarginal gyrus (rSMG) and the right temporoparietal junction (rTPJ) during self-other distinction, could not be replicated. This may be due to the modest sample size in addition to the approach taken during data analysis, as a block design modeling long stretches of each trial may have not been able to reveal small changes in activation during specific events of the game. Given the complexity of this fMRI paradigm, additional analyses should be performed to maximize the differences between the experimental conditions.

Keywords: Empathy, Self-Other Distinction, Altercentric Bias, Emotional Egocentricity Bias, Cyberball, Social Exclusion, Autism Spectrum Disorder

German Abstract

Empathie bezeichnet die menschliche Fähigkeit, die Gefühlszustände anderer Menschen indirekt zu erleben und kann in zwei Hauptkomponenten unterteilt werden: *affektive Empathie* (die Fähigkeit, die Gefühle anderer zu spüren) und *kognitive Empathie* (die Fähigkeit, mentale Zustände anderer zu erschließen). In diesem Kontext ist die Fähigkeit, zwischen eigenen und fremden inneren Zuständen zu unterscheiden (*Self-Other Distinction*, SOD), essentiell. Diese Studie zielte darauf ab, Situationen zu untersuchen, in denen Self-Other Distinction beeinträchtigt ist, was zu Fehlern bei der Einschätzung der eigenen Gefühle sowie der Gefühle anderer führen kann. Gleichzeitig sollten die neuronalen Mechanismen, die diesem Prozess zugrunde liegen, mittels funktioneller Magnetresonanztomographie (fMRT) untersucht werden. Wir verwendeten ein virtuelles Ballspiel um interaktive soziale Situationen hervorzurufen und induzierten positive und negative Gefühlszustände, indem die Spieler systematisch ein- und ausgeschlossen wurden. Anschließend mussten die Versuchspersonen abwechselnd ihre eigenen Gefühle oder die eines anderen Spielers einschätzen. Dieses Paradigma wurde verwendet um sowohl zwanzig neurotypische erwachsene Männer (Studie 1) als auch 15 Männer mit Autismus-Spektrums-Störung (ASS), im Vergleich zu 15 Kontrollpersonen, (Studie 2) zu untersuchen. Die Ergebnisse von Studie 1 zeigten Folgendes: In inkongruent Spielsituationen, also wenn eine Person inkludiert (d.h. in einem positiven Gefühlszustand) und die andere Person exkludiert (d.h. in einem negativen Gefühlszustand) war, verschoben sich die Gefühlsbewertungen in Richtung des affektiven Zustands der nicht-bewerteten Person. Wenn es also darum ging, die eigenen Gefühle zu beurteilen, wurden die Versuchspersonen von den Gefühlen des Gegenübers beeinflusst, ein Effekt der sich allozentrischer Fehler (*Altercentric Bias*, AB) nennt. Umgekehrt beeinflusste der eigene affektive Zustand die Einschätzung der Gefühle der anderen Person, was sich emotionaler Egozentrizitätsfehler (*Emotional Egocentricity Bias*, EEB) nennt. Studie 2 bestätigte die Existenz eines EEB sowie eines AB, jedoch zeigten sich keine Gruppenunterschiede, Versuchspersonen mit ASS zeigten also ähnlichen Ausprägungen in Self-Other Distinction und kognitiver Empathie wie neurotypische Kontrollpersonen. Die Ergebnisse der Neuro-Bildgebung waren generell uneindeutig. Ergebnisse aus vergangenen Studien, die bei SOD starke Aktivierungen im rechten Gyrus supramarginalis (rSMG) und im rechten temporoparietalen Übergang (rTPJ) fanden, konnten nicht repliziert werden. Gründe hierfür könnten sowohl die bescheidene Stichprobengröße als auch die Art der Datenanalyse sein, da ein Block-Design gewählt wurde, das längere Abschnitte eines Durchgangs modellierte und somit bei bestimmten Ereignissen des Spiels entstehende, kleine Änderungen in der Aktivierung nicht entdeckt haben könnte. Aufgrund der Komplexität dieses fMRT Paradigmas sollten weitere Analysen durchgeführt werden, um die Unterschiede zwischen den Experimentalkonditionen zu maximieren.

Schlüsselwörter: Empathie, Self-Other Distinction, Allozentrischer Fehler, Emotionaler Egozentrizitätsfehler, Cyberball, Soziale Exklusion, Autismus-Spektrums-Störung

Supplementary Material

Additional Tables

Table A1. *Two-sided Spearman correlations between the mean EEB, the mean AB, trait empathy, alexithymia and autistic traits for Study 1.*

	AB	EEB	Autistic Traits
Trait Empathy			
Fantasy	.420	.350	-.203
Empathic Concern	.124	.349	-.332
Perspective Taking	.431	.816	-.564**
Personal Distress	-.214	.819	.362
Alexithymia			
Difficulty Identifying Feelings	-.225	-.283	.344
Difficulty Describing Feelings	.340	-.002	.124
Externally Oriented Thinking	-.185	.095	.445*
Autistic Traits	-.263	.293	---

Note. Significant correlations are marked with one asterisk for ($p < .05$) and two asterisks for ($p > .001$). Sample size for Study 1 was $n_1 = 20$.

Table A2. *Two-sided Spearman correlations between the mean EEB, the mean AB, trait empathy, alexithymia and autistic traits for Study 2.*

	AB	EEB	Autistic Traits
Trait Empathy			
Fantasy	.236	-.107	-.421*
Empathic Concern	1.49	-.152	-.256
Perspective Taking	.314	-383*	-.599**
Personal Distress	-.265	.098	.086
Alexithymia			
Difficulty Identifying Feelings	-.023	.021	.647**
Difficulty Describing Feelings	.127	.158	.626**
Externally Oriented Thinking	-.229	.248	.459*
Autistic Traits	-.135	2.67	---

Note. Significant correlations are marked with one asterisk for ($p < .05$) and two asterisks for ($p > .001$). Sample size for Study 2 was $n_2 = 30$.