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„Examining functional connectivity of the temporoparietal junction and its relationship with self-reported empathy, alexithymia and autistic traits"


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## Theoretical and Empirical Background

In our everyday life, we interact with other people and face a variety of social situations. In order to successfully manage these social situations, the ability to understand mental states and feelings of other people is crucial. Based on the evidence from the psychological and neuroscientific research in the field of social cognition, the distinction between the cognitive and the affective route of understanding others can be made (Hoffmann, 2015; Kanske, Boeckler, Trautwein, & Singer, 2015; Singer, 2006). The cognitive route refers to the ability to understand the mental states of others, their beliefs and intentions, and is associated with such processes as theory of mind (ToM), cognitive perspective taking and mentalizing, which are often used as synonyms (Frith & Frith, 2006; Saxe & Kanwisher, 2003; Saxe & Wexler, 2005). On the other hand, the affective route refers to emotional understanding and is associated with the multidimensional psychological construct of empathy (De Vignemont & Singer, 2006; Singer, 2006; Shamay-Tsoory, 2011). In recent years a lot of research focused on the investigation of empathy and its underlying mechanisms. The definition of empathy varies across studies, and despite the fact that there is no unified definition, three main aspects of empathy can be described: 1) the ability to respond to the emotional state of others and share their feelings, 2) the cognitive ability to understand the feelings of others by taking their perspective, and 3) the ability to differentiate between one's own feelings and those of other people and to maintain this distinction (Decety & Jackson, 2006; Lamm, Batson, & Decety, 2007; Schulte-Rüther, Markowitsch, Fink, & Piefke, 2007). Thus, on the one hand, the affective empathy system and related processes, such as emotional contagion and emotion recognition, and on the other hand, the cognitive empathy system, based on higher cognitive processing and ToM, can be distinguished (Baron-Cohen & Wheelwright, 2004; Gonzalez, Shamay-Tsoory, & Bruene, 2013; Singer & Lamm, 2009; Shamay-Tsoory, 2011; Shamay-Tsoory, Aharon-Peretz, & Perry, 2009; Perry & Shamay-Tsoory, 2013).

**Affective empathy and the underlying neural mechanisms.** Broadly, the affective empathy can be defined as an appropriate affective response to an affective state of the other person (Baron-Cohen & Wheelwright, 2004). Based on the perception-action hypothesis in the motor domain (Prinz, 1997), claiming that the observation of someone's behaviour automatically evokes representations of this behaviour in oneself and that these representations are associated with activations in corresponding motor areas, Preston and de Waal (2002) presented a perception-action model of empathy. According to this model, when observing the affective states of others, the representations of these states are automatically activated in

oneself, resulting in autonomic and somatic responses, and affect sharing (Preston & de Waal, 2002). Further research on mirror neuron system (MNS) and simulation mechanisms, demonstrated that this mirroring mechanism can account for shared representations not only in the motor domain, but also in the domain of affective empathy and emotion recognition (for a review see Gallese, Eagle, & Migone, 2007; Gallese, Keysers, & Rizzolatti, 2004). Thus, studies have demonstrated that observing and imitating the emotional facial expressions of other people leads to the overlapping activations in the primary motor cortex, inferior frontal gyrus (IFG), superior temporal sulcus (STS) as well as anterior insula (AI) and amygdala (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Pfeifer, Iacoboni, Mazziotta, & Dapretto, 2008). These findings suggest that together the MNS, AI and limbic structures play a crucial role in understanding the emotions of others (Carr et al., 2003; Pfeifer et al., 2008). Moreover, Schulte-Rüther et al. (2007) reported in their study the bilateral activation of the IFG, when observing the emotional facial expressions and attributing the emotional states and emphasized that this activation was stronger in the self-attribution condition. They also found a positive correlation between the trait empathy, assessed by the Balanced Emotional Empathy Scale (Mehrabian, 1996), and the activations in the IFG and left superior temporal sulcus (lSTS) (Schulte-Rüther et al., 2007). Another study on neurological patients with lesions in the IFG, indicated that lesions in this region are associated with impairments in both, the emotion recognition, assessed by the experimental task, and the affective empathy, measured by the empathic concern and personal distress subscales of the Interpersonal Reactivity Index (IRI; Davis, 1980, 1983; Shamay-Tsoory et al., 2009). Jabbi, Swart, and Keysers (2007) investigated affective empathy by presenting the subjects with facial expressions of gustatory disgust or pleasure, or neutral facial expressions, measuring the activations in the AI and frontal operculum, associated with such experiences, and by correlating the self-reported trait empathy, assessed by the IRI, with these activations. They found that the magnitude of the activation of the AI and frontal operculum, correlated with the scores on the personal distress and fantasizing subscales of the IRI (Jabbi et al., 2007). Moreover, the account of shared representations was also investigated in the domain of empathy for tactile experiences and it was shown that the mirroring mechanism is involved in empathy for touch (Blakemore, Bristow, Bird, Frith, & Ward, 2005; Keysers et al., 2004). In the recent study, Lamm, Silani and Singer (2015), demonstrated that distinct networks are involved in the experience of pleasant and unpleasant touch by oneself (medial orbitofrontal cortex (mOFC) and frontal insular cortex, respectively), and that emphasizing with this pleasant and unpleasant touch experience is associated with the shared activation in these networks.

Further evidence for the role of shared representations in affective empathy are coming from investigations in the domain of empathy for pain. Recent studies and meta-analyses showed, that the observation of other's experience of pain activates the neural network partly overlapping with the network, underlying the experience of pain by oneself (Bernhardt & Singer, 2012; Decety & Lamm, 2006; Lamm, Decety, & Singer, 2011; Singer & Lamm 2009). Based on the results from experimental studies, the bilateral AI and anterior cingulate cortex (ACC), were identified as core regions for empathy for pain (Singer et al., 2004; Singer et al., 2006). Furthermore, it was shown that activation in the left AI and posterior ACC, was also correlated with self-reported empathy (Singer et al., 2004). Jackson, Brunet, Meltzoff, and Decety (2006) reported in their study partly overlapping activations, when imagining painful experiences for oneself or the other person. They demonstrated the overlapping activation in the AI, ACC (specifically Brodmann area 32; BA 32) and parietal operculum for both (self and other) conditions, but they also found distinct activations, depending on the experimental condition (Jackson et al., 2006). Recently a meta-analytical study provided further evidence for the involvement of the AI and ACC in empathy for pain (Lamm, Decety, & Singer, 2011). The results of this meta-analysis suggested that the bilateral insula, the anterior midcingulate cortex (aMCC) and the posterior ACC play a crucial role in the empathy for pain (Lamm et al., 2011). The involvement of these regions in the experience of pain by oneself and in empathy for others' pain, supports the shared representations hypothesis. On the other hand, the fact that the networks only partially overlap, emphasizes that further processes, such as self-other distinction, play an important role in experiencing empathy (Jackson et al., 2006; Lamm et al., 2011).

When talking about empathy it is important to make a distinction between affective empathy and related phenomena such as emotional contagion, mimicry, empathic concern, compassion and sympathy. The main difference between empathy, emotional contagion (tendency to automatically adopt emotional states of others) and mimicry (automatic imitation of facial expressions of others), is the distinction between oneself and another person, as an underlying mechanism for empathy (Decety & Jackson, 2006; Singer & Lamm, 2009; Singer, 2012). Furthermore, empathy differs from empathic concern or compassion, in terms of shared emotions. While empathising with someone we are sharing the same emotions as the other person, while when experiencing empathic concern or compassion, we are experiencing the feelings of concern and care for the person and are driven to help them (Singer & Lamm, 2009; Singer, 2012). These phenomena are closely related to the affective empathy, and therefore the self-report questionnaires, measuring affective empathy, include these as subscales. For

instance, the affective empathy assessed by the Empathic Concern and Personal Distress subscales, which reflect the other and self-oriented feelings, respectively (Davis, 1980, 1983). Another example, is the Questionnaire of Cognitive and Affective Empathy (QCAE), which measures the affective empathy by three subscales: Emotional Contagion, Proximal and Peripheral affective Responsiveness (Reniers, Corcoran, Drake, Shryane, & Völlm, 2011).

**Cognitive empathy and the underlying neural mechanisms.** Besides the affective component of empathy, the cognitive empathy, which can be defined as the ability to understand the mental states of others and by taking their perspective, can be distinguished (Shamay-Tsoory, 2011; Perry & Shamay-Tsoory, 2013). Cognitive empathy is suggested to be closely related to ToM or mentalizing, which is the ability to understand and predict the behaviour of other people, by reading and understanding their beliefs, intentions, desires, etc. (Frith & Frith, 2006; Saxe & Kanwisher, 2003; Saxe & Wexler, 2005; Völlm et al., 2006). Furthermore, within ToM the distinction between the affective ToM (the ability to make inferences emotions and feelings) and the cognitive ToM (the ability to make inferences about mental states) can be made (Schlaffke et al., 2015; Shamay-Tsoory & Aharon-Peretz, 2007). Even though definitions of cognitive empathy and ToM are very similar, some authors make a distinction between these processes. For instance, when talking about cognitive empathy Reniers et al. (2011) make the emphasis on the attribution of the emotional states rather than the cognitive states. On the other hand, Perry and Shamay-Tsoory (2013), proposed that cognitive empathy relies on both the affective and the cognitive ToM. Despite the fact that definitions of both cognitive empathy and ToM may vary from study to study, these processes are closely related and rely on perspective-taking and self-other distinction mechanisms.

The neural underpinnings of ToM have been largely investigated and the “mentalizing network” has been revealed. This network encompasses several brain regions, such as medial prefrontal cortex (mPFC), superior temporal sulcus (STS), temporoparietal junction (TPJ) and temporal poles (TP), which are associated with the different processes involved in ToM (Gallagher & Frith, 2003; Frith & Frith, 2006; Shamay-Tsoory, 2011). So, for instance, STS is associated with such processes as observation and monitoring of gaze, visual perspective-taking and decoding the social signals (Bukowski & Lamm, 2018; Frith & Frith, 2003; Molenberghs, Johnson, Henry, & Mattingley, 2016). The activity of the TP is associated with the encoding and storage of knowledge about specific people and situations, semantic and episodic memory retrieval, as well as with ToM (Frith & Frith, 2003; Gallagher & Frith, 2003; Olson, Plotzker, & Ezzyat, 2007). Furthermore, depending on the modality of the task, various

further regions, such as amygdala, OFC and IFG were shown to be activated and involved in ToM (Gallagher & Frith, 2003; Mar, 2011; Molenberghs et al., 2016; Völlm et al., 2006).

One of the regions widely discussed as crucial in ToM is the mPFC. In their review article, Gallagher and Frith (2003) proposed that the mPFC, specifically the anterior paracingulate cortex, plays a crucial role in mentalizing. Further studies on ToM suggested the functional segregation of the mPFC region (for a review see Amodio & Frith, 2006). For instance, Mitchell, Macrae, and Banaji (2006) reported that attribution of mental states to other people, which are considered similar to oneself, as well as the references about one's own mental states, are associated with the activity in the ventral parts of the mPFC. On the other hand, when attributing the mental states of dissimilar others, the activation changes in dorsal parts of the mPFC were observed (Mitchell et al., 2006). In a review article, Amodio and Frith (2006) discussed results of various experimental studies and proposed a functional segregation model of the medial frontal cortex, where its anterior part and the paracingulate cortex specifically, were associated with mentalizing. Even though the studies mentioned previously, mostly investigated the involvement of the mPFC in the context of cognitive mentalizing, there is evidence that the networks underlying the judging of the emotional states of oneself and other people, partially overlap in the mPFC (Ochsner et al., 2004). Furthermore, among other regions, two regions in the mPFC were found to be activated in the cognitive and emotional perspective-taking tasks (Hynes, Baird, & Grafton, 2006). Recent meta-analytical studies investigated regions involved in ToM and concluded that the mPFC is one of the regions activated across different ToM tasks and that distinct parts of this region show different connectivity patterns and are involved in different processes, such as perspective-taking, self-referential processing, and reward-related processing, etc. (Bzdok et al., 2015; Molenberghs et al., 2016).

**TPJ and empathy.** Another region involved in cognitive empathy and the ToM and activated across different tasks, is the TPJ. The TPJ is a region located in-between the temporal and the parietal lobe and encompasses the posterior part of the superior temporal gyrus (STG), the angular gyrus (AG), the supramarginal gyrus (SMG), and parts of the lateral occipital cortex (Bukowski & Lamm, 2017; Decety & Lamm, 2007; Mars et al., 2012). In recent years a wide range of research focused on the TPJ and its involvement in empathy and ToM, as well as such processes as self-other distinction, attention reorienting and agency. The activity of the TPJ was associated with perspective-taking in the cognitive and emotional domains and the attribution of mental and emotional states to other people (Hynes et al., 2006; Ruby & Decety 2003, 2004; Saxe & Kanwisher, 2003; Saxe & Wexler, 2005). More specifically, some studies

claimed a selective role of the right TPJ (rTPJ) in self-other distinction (Ruby & Decety, 2003, 2004; Saxe & Wexler, 2005; Schulte-Rüther et al., 2007), while other studies suggested the involvement of the left TPJ (lTPJ) and demonstrated that lesions in the lTPJ lead to impairments in the attribution of mental states to others (Samson, Apperly, Chiavarino, & Humphreys, 2004). Also, meta-analytical studies investigating the neural underpinnings of the ToM, identified the TPJ as one the regions activated across different ToM tasks (Mar, 2011; Molenberghs et al., 2016; Schurz, Radua, Aichhorn, Richlan, & Perner, 2014). Furthermore, the role of the rTPJ in the control of automatic imitative behaviour and visual perspective-taking, was also suggested in the domain of action perception (Brass, Ruby, & Spengler, 2009; Santiesteban, Banissy, Catmur, & Bird, 2012). Also, it was proposed, that the self-other distinction contributes to the monitoring and control of shared representations (Brass et al., 2009).

Mitchell (2009) claimed that when mentalizing about others, people use oneself as a reference, but to do so successfully the ongoing distinction between one's own cognitive and emotional states and those of others is crucial, and the TPJ plays an essential role in this process of self-and-other distinction. In the emotional domain the self-other distinction was investigated in recent experiments conducted by Silani (2013) investigating the neural underpinnings of the egocentricity bias (EEB). They demonstrated that when empathising with others, people tend to use their own emotional states as a reference, which in case of a mismatch between one's own emotions and those of others, can lead to the EEB (Silani et al., 2013). In the subsequent MRI and TMS experiments, it was shown that posterior rSMG was involved in overcoming the EEB, i.e. the tendency to egocentrical judgements, and that reduced response time increase the EEB (Silani et al., 2013). Another study investigating the EEB also reported rSMG as a region crucially involved in overcoming the EEB (Steinbeis, Bernhard, & Singer, 2015). Furthermore, based on the functional connectivity analysis, Steinbeis et al. (2015) demonstrated that in adults, but not in children, the rSMG was strongly connected to the left dorsolateral prefrontal cortex (lDLPFC), and that children were more egocentrically biased overall. These and further findings suggested the age-related differences, associated with cortical maturation processes, in overcoming the EEB (Riva, Triscoli, Lamm, Carnaghi, & Silani, 2016; Steinbeis et al., 2015). Authors found different connectivity patterns of the rSMG and the rTPJ and concluded that rSMG plays a crucial role in self-other differentiation in the emotional domain, but not in the cognitive domain (Steinbeis et al., 2015). In line with these results, another study reported distinct connectivity profiles of the rSMG and the rTPJ, and furthermore, showed that in patients with autism spectrum disorder (ASD) the rSMG network

compared to the rTPJ was intact (Hoffmann, Koehne, Steinbeis, Dziobek, & Singer, 2016). Thus, taken together, studies showed that the ability to distinguish between one's own representations and those of others – self-other distinction – is a crucial mechanism underlying ToM and empathy (for a review on self-other distinction see Lamm, Bukowski, & Silani, 2015; Steinbeis, 2016).

Besides reported activations in studies in the domain of social cognition, rTPJ activity was associated with the ventral attentional network, and more specifically, with reorienting of attention to the behaviourally relevant and unexpected stimuli (Corbetta, & Shulman, 2002; Corbetta, Patel, & Schulman, 2008). Because rTPJ activation is associated with both, social cognition and attentional processes, the question, what is the relationship between these two processes, and the question, whether the same or distinct regions within the rTPJ are activated during both processes, were widely investigated. In general, there is a distinction between the fractioning and the overarching view (for a review see Cabeza, Ciaramelli, & Moscovitch, 2012). In the first case, different subregions within the broader brain region subserve distinct functions, whereas in the second case, these subregions exist, but subserve just an aspect of the more general function (Cabeza et al., 2012). Studies and meta-analyses, investigating the role of rTPJ in social cognition and attention reorienting, found an overlap in the activations in the rTPJ, suggesting that high-level processes of social cognition rely on the low-level computational processes, also involved in attention reorienting (Bzdok et al., 2013; Decety & Lamm, 2007; Mitchell, 2008). Even though there was a substantial overlap in the activations, differences in activations were also found, with more posterior extended activity during ToM (Decety & Lamm, 2007). Overall, these results suggest that rTPJ is not selective only for ToM, and support the overarching view (Cabeza et al., 2012). On the other hand, another meta-analysis reported the overlap in activations was small and peripheral, arguing that distinct regions of rTPJ are involved in ToM and attention reorienting (Scholz, Triantafyllou, Whitfield-Gabriel, Brown, & Saxe, 2009).

More recent studies, investigated TPJ and showed the cytoarchitectonic and functional segregation within this region, with subregions showing different functional connectivity patterns (Bzdok et al., 2013; Caspers et al., 2006; Cohen, 2008; Krall et al., 2015; Kubit & Jack, 2013; Mars et al., 2011, 2012). So, using structural and functional connectivity analysis, Mars et al., (2012) showed three separate regions within TPJ: dorsal cluster in the intraparietal lobe (IPL), ventral anterior TPJ (TPJa) and posterior TPJ (TPJp) clusters. Moreover, these clusters showed different connectivity patterns, with IPL being strongly connected with areas associated with decision-making, task exploration and response strategy changing processes,

TPJa being strongly connected with areas associated with attentional processes, and TPJp being strongly connected witch areas associated with social cognition (Mars et al., 2011, 2012). Other studies also suggested functional segregation within rTPJ, and identified the anterior cluster, which was functionally associated with attentional processing, and the posterior cluster, functionally associated with social cognition and memory processing (Bzdok et al., 2013; Krall et al., 2015). Kubit and Jack (2013) identified three separate peaks of activation in the rTPJ and proposed a distinction into the posterior region (AG), associated with social cognition, and the anterior region (SMG), associated with target detection, and the region located between AG and SMG, associated with attention reorienting. The networks of the anterior rTPJ and the posterior rTPJ were suggested to be anticorrelated (Bzdok et al., 2013; Kubit & Jack, 2013). Furthermore, based on the results from the meta-analysis, Krall et al. (2015) suggested that the anterior rTPJ is involved in social cognition, as well as in attentional processing. Subsequent stimulation study, supported these results, by demonstrating that inhibitory stimulation of the anterior rTPJ resulted in the impaired performance in the attention reorienting task, as well as in the false belief task (Krall et al., 2016). Thus, taken together, the rTPJ is a region, where at least two subregions can be distinguished, which showed distinctive connectivity patterns, and which are involved in ToM, empathy and attentional processing.

**Empathy, alexithymia and autism spectrum disorders (ASD).** Most of the studies described before were performed with healthy participants. In empathy research, however, the investigation of disorders, such as the ASD, the related deficits and the underlying mechanisms, can be very informative. According to the Diagnostic and Statistical Manual of Mental Disorders (DSM-V; American Psychiatric Association, APA, 2013) the ASD is an early onset developmental disorder associated with deficits in social interaction, communication impairments and a repetitive pattern of behaviour and interests, and often accompanied by intellectual and language delay (for a review see Frith & Happe, 2005). It is important to note, that in the previous edition of the DSM (DSM-IV, APA, 1994) Asperger disorder or Asperger syndrome (AS), which is a form of autism but without impairments of language and intellectual development, was defined as a distinct diagnosis. Furthermore, in the research the diagnosis of high-functioning autism (HFA) is used as a synonym to the AS.

Research in the field of social cognition with ASD individuals showed that ASD is associated with deficits in empathy and its facets. As it was mentioned above, cognitive empathy is closely related to ToM and relies on mechanisms of self-other distinction. Experimental studies demonstrated that individuals with ASD showed deficits in cognitive empathy and difficulties in accomplishing the ToM tasks (for a review see Frith, 2001; Frith &

Happe, 2005). Studies investigating the attribution of mental states, showed that individuals with ASD experienced difficulties in giving accurate attributions and reported decreased activation in the mentalizing network, including mPFC, TP and TPJ regions (Castelli, Frith, Happe, & Frith, 2002). Further research demonstrated deficits in the attribution of mental states due to altered rTPJ functioning in individuals with ASD, which correlated with the severity of the social impairments (Lombardo, Chakrabarti, Bullmore, MRC AIMS Consortium, & Baron-Cohen, 2011). Moreover, non-typical involvement of the rTPJ in the processing of the averted gaze versus direct gaze in HFA individuals was reported in the study, researching the processing of socially relevant cues, such as gaze direction (Pitskel et al., 2011). Further studies, suggested structural and functional alterations in the region of the TPJ, such as decreased gray matter volume, altered functional and structural connectivity profile (David et al., 2014; Kana, Libero, Hu, Deshpande, & Colburn, 2012; Mueller et al., 2013). Also, a recent study investigating functional connectivity of the rTPJ in the ASD individuals, reported reduced connectivity of this regions to the lTPJ, posterior cingulate cortex (PCC) and mPFC, but no alterations in the distinct SMG-network, proposing deficits in the self-other distinction in the cognitive domain in ASD (Hoffmann et al., 2016).

Studies, using the self-report questionnaires to assess empathy, demonstrated that individuals with ASD score lower on the cognitive empathy scales. For instance, Baron-Cohen and Wheelwright (2004) developed a self-report instrument, Empathy Quotient (EQ), and reported that individuals with AS/HFA scored lower than healthy individuals. Furthermore, it was shown that participants with ASD, compared to healthy individuals, scored lower on the cognitive subscales of IRI, and scored equivalently on empathic concern subscale, and scored higher on personal distress subscale, indicating that ASD individuals experience higher emotional arousal and personal discomfort in social situations (Dziobek et al., 2008; Fan, Chen, Chen, Decety, & Cheng, 2014; Rogers, Dziobek, Hassenstab, Wolf, & Convit, 2007). Thus, these studies further support the assumption that individuals with ASD show deficits in cognitive, but not in affective empathy.

Although, research suggests that individuals with ASD might not have deficits in affective empathy, they do not show the normal empathic response either. This impaired empathic response can be explained through deficits in ToM and perspective-taking (Baron-Cohen, 2002). In a case study with ASD patients, it was proposed that deficits in empathy can be explained by dysfunction in integration of cognitive and affective information about other's and the social situation (Shamay-Tsoory, Tomer, Yaniv, & Aharon-Peretz, 2002). Another explanation for the deficits in empathy in ASD is the imbalance between cognitive empathy,

which is low, and the emotional sensitivity, which is too high and leads to overarousal, so that individuals with ASD show aversive social behaviour in order to avoid this overarousal (Smith, 2009).

There is further evidence that deficits in the affective domain are associated not with the diagnosis of ASD, but with the co-occurring alexithymia (for a review see Bird & Cook, 2013). Alexithymia, can be defined as a condition associated with difficulties in identifying, describing and analyzing emotions, as well as associated with an impaired fantasy and emotional experience (Taylor, Ryan, & Bagby, 1985; Vorst, & Bermond, 2001). It was shown that self-reported alexithymia is correlated with the lack of empathy, and that deficits in emotional awareness can be linked to the reduced activity in the AI (Silani et al., 2008). In line with this study, further research, comparing individuals with ASD and healthy participants, both groups containing individuals with low as well as individuals with high alexithymia, reported that the degree of alexithymia and not the ASD diagnosis is associated with reduced empathic response and reduced AI activation (Bird et al., 2010).

Alexithymia and deficits related to it were also investigated in non-autistic individuals and was associated with impaired emotion recognition, empathy and mentalizing (for a review see Bird & Cook, 2013; van der Velde et al., 2013). According to Vorst and Bermond (2001) alexithymia can be distinguished into the cognitive and the affective dimension. The cognitive dimension is associated with difficulties in identifying, describing and analysing emotional states and reaction, and their origin, whereas the affective dimension, relates to deficits in emotional experience and the ability to fantasize (Vorst & Bermond, 2001). Correlation studies using self-report instruments revealed a negative correlation between the degree of alexithymia and empathy (Bird et al., 2010; Silani et al., 2008). Similar to these findings, individuals with alexithymia scored lower on perspective-taking and empathic concern subscales of IRI, indicating lower empathy, and scored higher on the personal distress subscale, indicating higher emotional arousal (Moriguchi et al., 2006). Furthermore, they also gave lower ratings of pain experience, when judging other people (Moriguchi et al., 2006).

On the neural level alexithymia is associated with alterations in the regions of so-called “affective representational system”, such as ACC, AI und amygdala (for a review see Bird, & Viding, 2014; Wingbermühle, Theunissen, Verhoeven, Kessels, & Egger, 2012). Although several neuroimaging studies investigated the neural underpinnings of alexithymia using different experimental tasks (positive and negative emotional facial expressions, stimuli depicting pain and painful situations) the results are inconclusive. There is debate regarding the neural underpinning and whether the alexithymia is characterized by the reduced activity

in the ACC and increased activations of the AI (Moriguchi et al., 2006), or by the opposite activations patter (van der Velde et al., 2013). Besides the higher activations in dorsal ACC and MCC in alexithymia, van der Velde et al. (2013) reported a valence-dependent activation pattern, with lower activation in the precuneus, left STG and the right insula for positive stimuli and lower activity in the amygdala, left premotor and dorsomedial PFC, as well as in the fusiform area and supplementary premotor area. Moreover, in the study, exploring the relationship between alexithymia and altruistic behaviour, higher alexithymia was linked to the reduced activation in the dorsal ACC and to decreased personal distress, which was associated with a reduced AI and TPJ activity (FeldmanHall, Dalgleish, & Mobbs, 2012).

## Objective

This thesis was conducted as a part of a larger research project investigating the neural mechanisms underlying the EEB. The project was based on the previous study by Silani et al. (2013), who developed a new experimental paradigm and demonstrated in a series of experiments, that activity in the rSMG can be associated with EEB and more specifically, that rSMG is crucial for overcoming this bias towards one's own affective state. Further studies also reported involvement of rSMG in overcoming the EEB, emphasizing the role of this region in self-other distinction in the emotional domain (Hoffmann et al., 2016; Steinbeis et al., 2015).

Self-other distinction is a key process in social cognition and is one of the mechanisms underlying empathy. On the neural level, self-other distinction is associated with the activation in the rTPJ (for a review see Lamm et al., 2016; Steinbeis, 2016). Previous studies, investigating the structural and functional properties of the rTPJ, reported segregation within this region and showed that rTPJ can be divided into at least two distinct subregions – the aTPJ and pTPJ, which show different connectivity patterns (Bzdok et al., 2013; Caspers et al., 2006; Cohen 2008; Hoffmann et al., 2016; Krall et al., 2015; Kubit & Jack, 2013; Mars 2011, 2012). Thus, based on previous findings, the first goal of the current thesis, was to investigate functional connectivity patterns of two regions of interest, namely rSMG and rAG. It was expected that both regions will show distinct functional connectivity patterns, with rSMG being coupled with regions involved in emotional, as well as in attentional processing, and rAG being connected with regions associated with mentalizing.

Furthermore, neuroimaging studies investigating the neural mechanisms of affective and cognitive empathy demonstrated partly overlapping as well as partly distinct networks involved in these processes. As discussed previously, one of the empathy components is affective empathy, which was related to the mechanism of shared representations (for a review

see Lamm & Majdandzic, 2015) and investigated in the studies on empathy for pain, emotion recognition and affect sharing (for a review see Shamay-Tsoory, 2011). Meta-analysis on studies on empathy for pain, on the one hand, revealed a common underlying network, consisting of bilateral AI, ACC and MCC, but, on the other hand, reported separate activation patterns for picture-based (anterior IPL, including SMG, and ventral premotor areas) and cue-based (TPJ, STS, mPFC, TP) experimental tasks used in the original study (Lamm et al., 2011). Further studies, also reported the network, encompassing bilateral AI, IFG, ACC and SMG, as an affective empathy network (Fan, Duncun, de Greck, & Northoff, 2011; Kanske et al., 2015; Shamay-Tsoory et al., 2009). Another empathy component is cognitive empathy, which relies on ToM, perspective-taking and self-other distinction mechanisms, was largely investigated and the core network, including ventromedial PFC (vmPFC), STS, TP, TPJ, PCC and precuneus, was identified (Fan et al., 2011; Kanske et al., 2015; Shamay-Tsoory et al., 2009). Moreover, studies including individuals with ASD and alexithymia, showed alterations within the TPJ and demonstrated distinct connectivity patterns of the anterior and the posterior TPJ (Castelli et al., 2002; Hoffmann et al., 2016; Lombardo et al., 2011). Deficits in empathy for individuals with alexithymia and ASD were further associated with impaired functioning of the AI, ACC as well as rTPJ (Bird et al., 2010; Hoffmann et al., 2016; Silani et al., 2008).

Another approach to investigate the neural correlates of empathy, besides using different experimental paradigms, is applying the self-report questionnaires. Several studies used self-report measures of empathy in their study design and reported correlations between neural activations and trait empathy. For example, scores on the Perspective-Taking subscale of IRI (Davis 1980, 1983) correlated with activation in TPJ (Hooker, Verosky, Germine, Knight, & D'Esposito, 2010), Empathic Concern and Personal Distress subscales were positively correlated with activity in IFG and AI (Jabbi et al., 2007; Kaplan & Iacoboni, 2006; Pfeifer et al., 2008; Shamay-Tsoory et al., 2009). A further study, reported correlations between empathy, measured by Empathy Quotient (EQ; Baron-Cohen & Wheelwright, 2004), and activations in the left IFG and premotor cortex, as well as a few further correlations between trait empathy and activations in the brain areas, depending on the task stimuli (Chakrabarti, Bullmore, & Baron-Cohen, 2006). Moreover, few studies investigated the relationship between self-reported trait empathy and gray matter volume, indicating that cognitive and affective empathy, can be associated with dissimilar gray matter density (Banissy, Kanai, Walsh, & Rees, 2012; Eres, Decety, Louis, & Molenberghs, 2015). Finally, it has been shown to be informative to combine resting state functional connectivity approach, which provides information about the functional connectivity between brain regions, and self-report measures.

One study, looked into the interaction between affective and cognitive empathy, assessed by IRI, and its relationship to the resting state networks, showing that greater affective empathy ability is associated with increased connectivity within networks, including right ventral AI and left OFC, left amygdala and rOFC, left amygdala and ACC, as well as rOFC and paracingulate gyrus, while greater cognitive empathy ability was linked to increased connectivity in the brainstem and STS, as well as in the ventral AI, brainstem and cerebellum networks (Cox et al., 2012).

Thus, based on literature research, a further goal of this thesis was an exploratory investigation of the relationship between self-reported cognitive and affective empathy, as well as self-reported alexithymia and autistic traits, and the connectivity within the rSMG and rAG networks, seeds which were proposed to be involved in self-other distinction in cognitive and affective domains, ToM, empathy and attentional processing. For these purposes the scores on the subscales of self-report instruments and the total scores on these instruments were correlated with whole-brain functional connectivity with two resting state networks, revealed in the first part of the analysis. Five self-report questionnaires were used in this thesis: IRI (Davis 1980, 1983), QCAE (Reniers et al., 2011), EQ (Baron-Cohen & Wheelwright, 2004), Bermond-Vorst Alexithymia Questionnaire (BVAQ; Vorst & Bermond, 2001) and Autism-Spectrum Quotient (AQ; Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). I expected that individual variations in affective trait empathy and cognitive trait empathy, assessed by IRI, QCAE and EQ, will be reflected in the connectivity within rSMG and rAG networks. Furthermore, I suggested that differences in the degree of alexithymia, measured by BVAQ, and the degree of autistic-like traits, measured by AQ, also will be displayed in the connectivity maps of rSMG and rAG.

## Method

### Study Design

This thesis was conducted within a research project, which aimed to investigate the neural underpinnings of the EEB. Based on the results from Silani et al. (2013) and using the experimental paradigm developed by them, this project investigated the effects of repetitive TMS of the rSMG and the vertex in a within-subject study design. The main goal of the study was the further understanding of the neural mechanisms underlying the EEB and the role of the rSMG in egocentricity in empathy.

The main focus of this thesis lies on the analysis of the resting state functional connectivity of two regions of interest: rSMG and rAG. A further goal was to correlate affective

and cognitive trait empathy, alexithymia and autistic-traits, assessed by self-report personality questionnaires, to these resting state networks.

**Participants**

Forty healthy right-handed female participants took part in the current study. All participants were recruited via social networks, online student forums and the online psychological research participation platform of the University of Vienna, as well as through flyers and advertisement in university department buildings. Since the EEB study was based on the previous work from Silani et al. (2013), and for the purpose of better comparability to the previous study, only female participants were recruited. Recent studies and reviews also reported gender differences in empathy and self-other distinction (Christov-Moore et al., 2014; Schulte-Rüther, Markowitsch, Shah, Fink, & Piefke, 2008; Tomova, von Dawans, Heinrichs, Silani, & Lamm, 2014). Moreover, studies showed that male and female participants score differently on the personality questionnaires used in this study (Baron-Cohen & Wheelwright, 2004; Baron-Cohen et al., 2001; Davis, 1980; Reniers et al., 2011; Vorst & Bermond, 2001). Thus, recruitment of just female participants eliminated gender as a potential cofounding variable. During the screening process, the standard MRI and TMS exclusion criteria were applied: current or previous neurological or psychiatric abnormalities, current or previous drug and alcohol abuse, previous neurosurgery, claustrophobia, pregnancy, the presence of any metallic objects on or inside the body, which cannot be removed, the presence of implants such as pacemaker or defibrillator, implanted brain electrodes, cochlear implants, etc. Only participants who met the criteria of the screening process, had normal or corrected-to-normal vision with contact lenses, and were right-handed, assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), were included in this study.

The final sample included in the analysis consisted of 34 right-handed, healthy females ($M_{age}$ = 22.03; *SD* = 3.44; age range: 18 to 31 years). Six participants had to be excluded from the analysis due to technical reasons and/or extensive movements during the obtaining of the resting state functional magnetic resonance imaging (rsfMRI) data. All participants signed the informed written consent form to participate in this study and received a monetary compensation (80 Euro) and the course credits (for undergraduate Psychology students) after completing two testing sessions. The study was conducted in accordance with the Declaration of Helsinki (1964) and the study protocol was approved by the ethics committee of the Medical University of Vienna.

**Procedure**

The study took place at the High Field MR Centre of the Medical University of Vienna. Before participants were invited to the study, they completed the online screening process by submitting the standard screening questionnaires for TMS and MRI used in the MR Centre of the Medical University of Vienna. Participants were also asked to fill in the personality questionnaires, described in the next section. The study consisted of two testing sessions, each of an approximate duration of three hours, with a one-week interval between the two sessions. In one case, a second testing session was postponed, thus there was an eight-day interval between testing sessions. Only one participant per testing session was invited. Because the visual-tactile paradigm developed by Silani et al. (2013), is an experimental paradigm that requires the testing of two individuals simultaneously, one confederate from our research team was assigned to each testing session. Participants and confederates did not know each other before the experiment and participated together in both testing sessions. Participants were unaware of the fact that the other person was part of the research team.

After the arrival participants and confederates were greeted by one of the two experimenters responsible for this part of the experiment. They were introduced to each other, were explained the experimental procedure and the experimental task, and were asked to complete the same standard screening questionnaires for TMS and MRI as they did online. The repeated completion of these questionnaires ensured that there were no changes in comparison to the first time and that participants did not consume any alcohol in the past 24 hours. Next, they were introduced to the rest of the research team and showed the MRI-scanner and TMS-Coil. In the scanning room the scanning procedure was explained in more detail (loud noise ratio in MR-Scanner, relevance to stay calm and try not to move while scanning, etc.). They were also shown the way TMS-Coil works and experienced a low intensity impulse on their hand, in order to get more familiar with the stimulation procedure. Moreover, they completed the practice trial of the experimental task on the computer, ensuring that they understood the task correctly. Afterwards, all participants were asked to sign the written consent form. Finally, participants and confederates were asked to change into the hospital scrubs and remove all metal objects (jewellery, hair clips, etc.).

For the scanning session participants stayed with the research team, while confederates were accompanied to the other scanning room, where they were supposedly tested. Right before the scanning, participants were asked to fill in the German version of the Positive and Negative Affect Schedule (PANAS; Krohne, Egloff, Kohlmann, & Tausch, 1996). The testing procedure for both session is shown in the Figure 1. The first testing session consisted of the

structural brain scan, finger-tapping task, single-perspective self-judgment and single-perspective other-judgment task, followed by the acquisition of the resting state for eight minutes. Next, participants were prepared for the TMS procedure outside the scanner. The individual motor threshold was defined, as well as the individual target stimulation site. Depending on the testing condition, using the TMS neuronavigation (Brainsight 2, Rogue Research Inc., Canada), the TMS-coil was manually positioned over the stimulation target (rSMG or vertex) and continuous theta burst stimulation (cTBS) for 40 seconds was applied. Afterwards participants were brought back to the scanner to perform the second part of the scanning procedure. In this part, the four blocks of double-perspective self- and other-judgment task were performed, with the eight minutes resting state acquisition period in between. The participants were pulled out of the scanner, asked to complete another PANAS questionnaire and brought to the changing room. At the end of the first testing session both (participant and confederate) were instructed to come to the next testing session in a week.

The procedure of the second testing session was similar to the first testing session, with the prestimulation scanning session comprising a diffusion tensor imaging (DTI) scan at the beginning, and exclusion of the finger-tapping task in this run. After completing the second testing session participants were debriefed and received the monetary compensation of 80 Euro. In addition, after both testing sessions participants were asked to complete the standard feedback TMS and MRI forms used in the MR Centre of the Medical University of Vienna. These feedback forms inquiring about the experiences and perceptions in the scanner, as well as about the occurrence of the possible side effects after the stimulation. Moreover, after the second testing session participants were also asked to fill the similarity feedback questionnaire (developed by our research team), which assessed their attitudes and feelings about the other person, who took part in the study (the confederate).

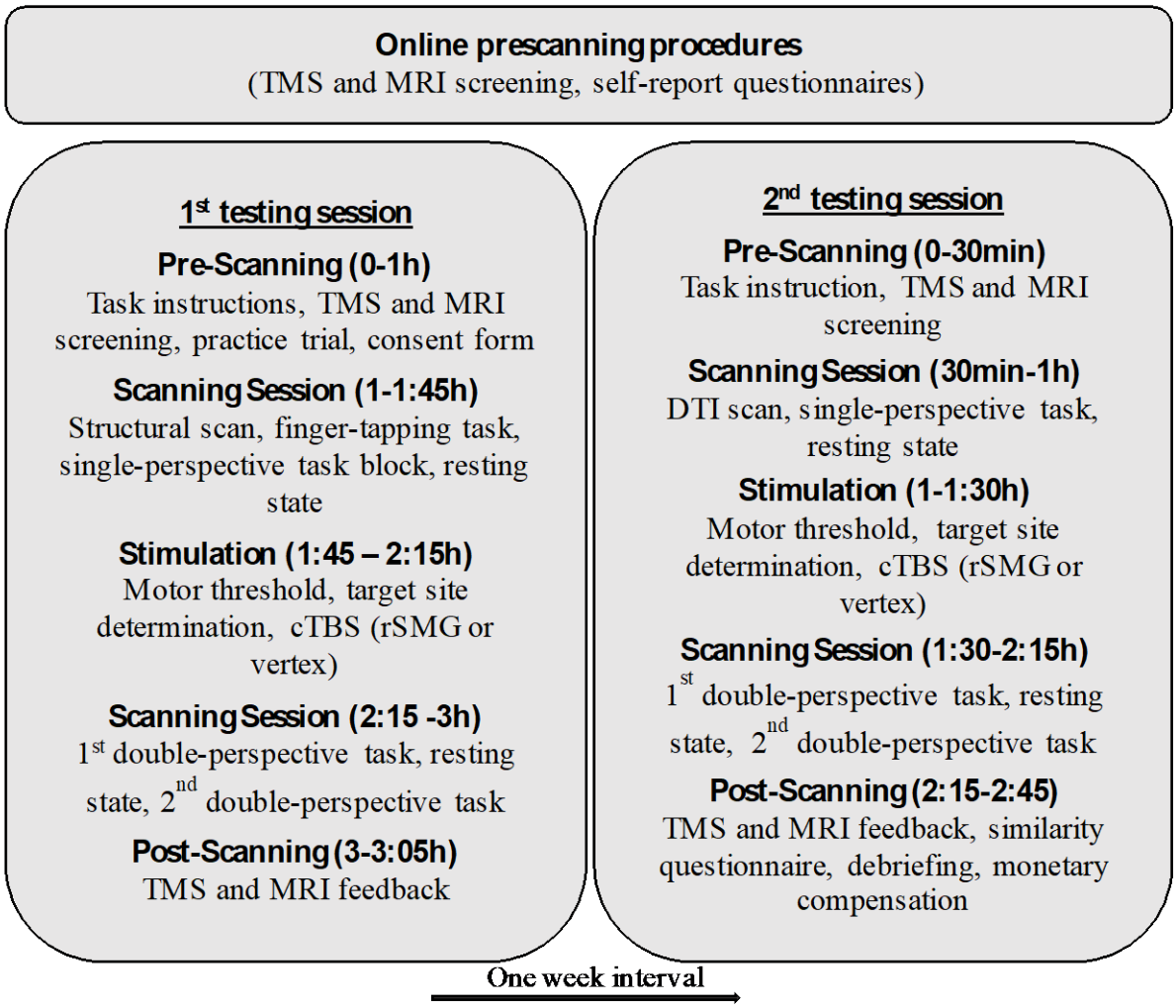


*Figure 1.* Research procedure flowchart. cTBS = Continuous Theta Burst Stimulation; DTI = Diffusion Tensor Imaging; MRI = Magnetic Resonance Imaging; rSMG = right supramarginal gyrus; TMS = Transcranial Magnetic Stimulation. Own Creation, 2018.

The description of the visual-tactile empathy touch task and its stimuli, as well as the description of the stimulation procedure and parameters lies beyond the scope of this thesis (for further details see Neumüller, 2017; Silani et al., 2013; Zechner, 2017). The analysis in this thesis is restricted to resting state data obtained in the first scanning session.

**Resting state functional magnetic resonance imaging (rsfMRI)**

rsfMRI is a method widely used in neuroscientific research to examine the relationships between brain regions. Biswal, Yetkin, Haughton, and Hyde (1995) demonstrated that during the resting state (the state of being awake and not performing a specific task) low frequency fluctuations (< 0.1 Hz) in blood oxygen level dependent (BOLD) signal in separate brain regions, associated with motor function, were correlated. Thus, based on this observation, it

was proposed that brain regions, which show correlations in low frequency fluctuations in BOLD signal, are functionally connected (for review see Bijsterbosch, Smith, & Beckmann, 2017; Cole, Smith, & Beckmann, 2010).

In recent years, this method was applied to investigate brain organization and intrinsic connectivity between brain regions, to identify and describe different resting state networks (for a review see Cole et al., 2010; Fox & Raichle, 2007). Furthermore, it was demonstrated that there is a relationship between RS networks and individual differences in self-reported personality traits (Cox et al., 2012; Di Martino et al., 2009). This method is considered a useful tool in clinical research (Bijsterbosch et al., 2017, p 6; Fox & Grecius, 2010).

One of the methods to investigate functional connectivity is a seed based correlation analysis, which results in the connectivity map of a defined region of interest and all the voxels in the brain (Bijsterbosch et al., 2017, p 52; Cole et al., 2010). In this study we performed the analysis for two separate a-priori defined seed regions, rSMG (MNI: 68, -38, 36) and rAG (MNI: 52, -52, 22). During resting state data acquisition, participants were not performing any tasks and were instructed to focus on the fixation cross on the screen, let their minds wander and not to think about anything in specific.

**Self-Report Questionnaires**

In order to assess the affective and cognitive trait empathy, as well as the affective and cognitive dimensions of alexithymia, five self-report questionnaires were used in this study. All questionnaires were provided in German and completed online before the first scanning session. The subscores for all subscales, as well as the total score for the questionnaires were calculated and included as regressors in the final analysis.

**Interpersonal Reactivity Index (IRI).** The IRI is a self-report instrument measuring empathy, constructed in the way that each of four subscales assesses the separate aspects of the multidimensional construct of empathy (Davis, 1980, 1983). The questionnaire consists of a total of 28 items, whereat each of four subscales consists of seven items rated on the Likert scale ranging from 0 (*does not describe me at all*) to 4 (*describes me very well*). The Perspective-Taking subscale refers to the ability to spontaneously take the perspective of other people. The Fantasy subscale assesses the individual's ability to identify themselves with fictional characters in movies, books, etc. The items of the Empathic Concern subscale measure the feelings of concern and compassion for others. And, finally, the items of the Personal Distress subscale obtain the feelings of personal anxiety and discomfort when observing the distress of others. The high scores on each subscale are indicative of higher abilities or higher

concern or distress measured by this subscale respectively. Davis (1983) proposed that perspective-taking subscale is highly associated with the cognitive dimension of empathy, while empathic concern and personal distress subscales directly assess the affective components and emotional responsiveness. Furthermore, it was suggested that individuals, who score higher on the fantasy subscale, tend to have higher verbal intelligence ability. Gender differences were also reported, where female participants scored higher on all four subscales.

The internal reliability (Cronbach's alphas) of the instrument reported by Davis (1980) ranged between .71 - .77. The Cronbach's alphas for the subscales for the sample of the current study ranged between .71 and .91.

**Questionnaire of Cognitive and Affective Empathy (QCAE).** The QCAE is a self-report tool developed to measure the affective and cognitive empathy (Reniers et al., 2011). The affective empathy is assessed by three subscales: (a) Emotion Contagion, reflecting the tendency to the automatic mirroring of the emotions of others, (b) Proximal Responsivity, measuring the level of the affective response to the emotional states of others in social situations, and (c) Peripheral Responsivity, assessing the level of the affective response to emotional situations in a less personal context than proximal responsivity subscale. The cognitive empathy is measured by two subscales: (d) Perspective Taking, assessing the tendency to intuitively take the point of view of others, and (e) Online Simulation, referring to the effortful process of taking the perspective of others to understand their feelings. The questionnaire consists of 31 items rated on 4-point Likert scale ranging from 1 (*strongly disagree*) to 4 (*strongly agree*). The scores for affective and cognitive empathy are calculated by summing the subscores for emotional contagion, proximal responsivity and peripheral responsivity for affective empathy, and perspective taking and online simulation for cognitive empathy. Higher scores are indicative of greater affective and cognitive empathy. The total empathy score is obtained by combining affective and cognitive empathy scores. Furthermore, gender differences were reported by Reniers et al. (2011), with females scoring higher than males on both cognitive and affective empathy.

The QCAE comprises items coming from the following empathy questionnaires, such as Interpersonal Reactivity Index (Davis, 1980, 1983), Impulsiveness Venturesomeness Empathy Inventory (Eysenck & Eysenck, 1978), Empathy Quotient (Baron-Cohen & Wheelwright, 2004) and the Hogan Empathy Scale (Hogan, 1969), meaning that scales can partly overlap (Reniers et al., 2011). This fact should be taken into consideration when comparing the results of QCAE to the results of other questionnaires. The validity of the five-

factor solution of QCAE was tested in a large sample and, furthermore, confirmed in other studies (Eres et al., 2015; Lockwood, Seara-Cardoso, & Viding, 2014; Reniers et al., 2011). The reported Cronbach's alpha for the subscales varied between .65 - .85 (Reniers et al., 2011). The Cronbach's alpha in the current study was good for Online Simulation ($\alpha$ = .83) and Perspective Taking ($\alpha$ = .83) subscales and for the cognitive empathy scale in total ($\alpha$ = .86). However, the calculated Cronbach's alphas for the subscales assessing the affective empathy (Proximal Responsivity, Emotional Contagion, Peripheral Responsivity) were .44, .46 and .72, respectively. The Cronbach's alpha for the total affective empathy scale was acceptable .66.

The Cronbach's alpha is a widely used reliability coefficient, but it was shown that this coefficient tends to be very low, when the sample size is small and with only a few number of items, which was the case in the current study (Charter, 2003; Yurdugül, 2008). Because the QCAE is a well-established and reliable instrument and because the Cronbach's alpha for the total affective empathy scale was acceptable, we decided not to exclude the affective empathy scale from our analysis.

**Empathy Quotient (EQ).** The EQ is a 60-item self-report instrument used for measuring empathy in adults (Baron-Cohen & Wheelwright, 2004). This questionnaire consists of 40 empathy-related items and 20 distractor filler items, where approximately half of the items are reverse formulated. The items are scored on a 4-point scale ranging between *strongly agree* and *strongly disagree*. The final scores are calculated by assigning zero points for non-empathetic answers, and one or two points for empathetic answers. It was shown that individuals with Asperger Syndrome/High Functioning Autism (AS/HFA) score lower on EQ than healthy controls (cut-off lower than 30 points), indicating the potential of application of the EQ in clinical settings. Furthermore, gender differences with women scoring slightly higher than men, were found.

Baron-Cohen and Wheelwright (2004) suggested no categorisation of items into affective and cognitive. However, in their study Lawrence, Shaw, Baker, Baron-Cohen, and David (2004) reduced EQ to 28 items, loading on three factors: cognitive empathy, emotional reactivity and social skills. In this thesis only, the cognitive empathy subscale (cEQ) comprising 11 items from EQ was used (Lawrence et al., 2004). The EQ is a well-validated self-administrated instrument with high test-retest reliability and high internal consistency ($\alpha$ = .92) (Baron-Cohen & Wheelwright, 2004; Lawrence et al., 2004). The calculated Cronbach's alpha for the cEQ in the current study was .85.

**Bermond-Vorst Alexithymia Questionnaire (BVAQ).** The BVAQ-40 is a self-report measure, which consists of 40 items and comprises five subscales measuring the cognitive and the affective dimensions of alexithymia (Vorst & Bermond, 2001). The cognitive dimension of alexithymia is measured by three subscales: (a) Identifying, which refers to the degree to which an individual is able to define the nature of one's own emotions, (b) Analyzing, which refers to the degree to which one is able to explain one's own emotional reactions, and (c) Verbalizing, which refers to the degree to which one is able to describe and communicate about one's own emotions. The affective dimension is assessed by two subscales: (d) Emotionalizing, which refers to the degree to which one is getting emotionally aroused during arousing events, and (e) Fantasizing, which describes the degree to which one is prone to day-dream and fantasize about virtual matter. Each subscale consists of eight items rated on 5-point Likert scale, ranging from 1 (*strongly agree*) to 5 (*strongly disagree*), where half of the items formulated positively, and another half is formulated negatively in reference to the trait. The high subscores on each of the subscales are indicative of alexithymia. Thus, higher scores on the cognitive dimension subscales indicate difficulties in identifying, analyzing and verbalizing one's own emotional reactions. Higher scores on the affective dimension subscales are indicative of lower abilities to fantasize and decreased emotional arousal when experiencing arousing events. Furthermore, Vorst and Bermond (2001) reported correlations between gender and subscales of BVAQ. This analysis revealed that the Emotionalizing subscale correlated with gender, i.e. women scored lower than men on this subscale.

The two-factor structure of BVAQ, with the affective and cognitive dimensions of alexithymia, was validated in different subject groups in five languages and the internal consistencies reported in this analysis varied between the groups, with the mean Cronbach's alpha of .78 (Bermond et al., 2007). The Cronbach's alpha values for the BVAQ subscales in our sample ranging between .82 to .88, showing high internal consistency.

**Autism-Spectrum Quotient (AQ).** The AQ is a self-report instrument assessing the degree to which the individuals of normal intelligence show autistic-like behaviour (Baron-Cohen et al., 2001). The AQ measures the abnormalities in five areas by the following subscales: Social Skill, Attention Switching, Attention to Detail, Communication and Imagination. Each subscale consists of ten items, resulting in a total of 50 items. The responses are scored on a 4-point scale ranging from *definitely agree* to *definitely disagree*. In order to prevent a response bias, approximately half of the items are formulated to evoke the positive or "agree" response, whereas the other items should produce a negative or "disagree" response. The scores are calculated for each subscale by assigning one point, when an individual shows

an autistic-like response. The sum of all subscale scores provides the total AQ score. Higher scores on each of the five subscales are indicative of poorer social skill, difficulties by attention switching, stronger attention to details, poorer communication skills and poorer imagination. The AQ was validated in different groups, including the general population and individuals diagnosed with AS/HFA, and the useful cut-off was set by 32+ total scores. Concerning the gender differences authors reported that males in the control group scored higher than females, but there were no significant differences in the scores in AS/HFA group. The internal consistency coefficient alpha for five subscales was also reported and varied from .63 to .77. (Baron-Cohen et al., 2001). Our analysis revealed that Cronbach's alpha for the Communication ($\alpha$ = .31) and Imagination ($\alpha$ = .35) subscales were very poor. The alpha for the other three subscales ranged between .53 and .61, showing questionable internal consistency. However, analysis of the consistency for the whole AQ revealed Cronbach's alpha of .73, which is acceptable. Taken into consideration the results of this analysis, the tendency of Cronbach's alpha being very low in small samples, and the fact that alpha for the whole questionnaire was acceptable, we included the AQ into the final analysis (Charter, 2003; Yurdugül, 2008).

**Image acquisition and data analysis**

**MRI Data.** The data were acquired on a 3-Tesla Siemens MAGNETOM Prisma whole-body MR scanner (Siemens Medical, Germany) equipped with a 32-channel head coil. First, the T1-weighted structural images were obtained (160 slices; 1.1mm slice thickness; matrix size = 256 × 256; TR = 2300ms; TE = 4.21ms; $1.0\times1.0\times1.1mm^3$ voxel size). Next, the functional resting state T2*-weighted images were acquired using a factor-3 multiband echo-planar imaging (EPI) sequence with 21 slices aligned parallel AC-PC plane and covering the whole brain (4mm slice thickness; matrix size = 96 × 96; TR = 600ms; TE = 35ms; $2.0\times2.0\times4.0mm^3$ voxel size). During the 8min acquisition time a total of 807 volumes were obtained. For the duration of the resting state data acquisition, participants were instructed to think of nothing in specific, let their mind wander but keep their gaze at the fixation cross.

Only the data of the first resting state acquisition from the first testing session was included into a final analysis.

**Data processing and analysis.** The acquired data were preprocessed and analysed using Analysis of Functional Neuroimages (AFNI; https://afni.nimh.nih.gov/), FMRIB Software Library (FSL 5; Analysis Group, FMRIB, Oxford, UK; https://fsl.fmrib.ox.ac.uk) and Statistical Parametric Mapping (SPM12; http://www.fil.ion.ucl.ac.uk/spm/software/spm12).

The data preprocessing and analysis procedures, as well as the software and applications used for the analysis, in this thesis were analogous to the analysis steps described in a TMS-study by Tik et al. (2017). As a first step of preprocessing, the resting state data were despiked using AFNI and slice-timing corrected with FSL 5, in order to correct for differences in time when slices were acquired. To correct for the low-frequency smooth signal, produced by the scanner and which is influencing the images, the data were bias field corrected using Advanced Normalization Tools (ANTs; http://stnava.github.io/ANTs/). Afterwards, the data were realigned, co-registered to the structural T1-weighted image and spatially normalized into standard MNI space using ANTs and FSL 5. As a last preprocessing step, using FSL 5 the data were smoothed by a 6-mm full-width at half-maximum (FWHM) Gaussian kernel. After the preprocessing, the data were further analysed, and the variance associated with Nuisance regressors, such as the motion parameters, the cerebrospinal fluid and the white matter mean signals, as well as the global mean signal, were removed from the data. It was reported that the first five components of principal component analysis are associated with physiological noise, and therefore regressing them out leads to reduction in noise (Behzadi, Restom, Liau, and Liu, 2007; Soltysik, Thomasson, Rajan, & Biassou, 2015; Weissenbacher et al., 2009). Furthermore, the Fast Fourier Transform (FFT) band pass filtering (0.009 – 0.08 Hz), reducing the low-frequency drift and high-frequency noise, and motion-scrubbing, described by Power, Barnes, Snyder, Schlaggar, and Petersen (2012), were applied.

Two seed regions of interest were defined by building a sphere (radius 3mm) around a-priori defined coordinates for rSMG (peak MNI: 68, -38, 36) and for rAG (peak MNI: 52, -52, 22). The coordinates for rSMG were chosen, based on the study by Silani et al. (2013) and coordinates for rAG were also based on the coordinates reported in the same study, but originally reported in the meta-analysis from Mar (2011).

Seed-based correlation analysis allows one to obtain the functional connectivity maps of voxels in the whole brain with the seed regions of interest. The means of the time series from the seed regions for each subject were extracted and correlated with the voxel of the whole brain, resulting in two functional correlation maps for every subject. Using the Fisher's Z-transformation, the individual's correlation values were transformed into Z-scores, resulting in *Z*-transformed maps. In order to investigate the relationship between the traits assessed by five personality questionnaires (IRI, QCAE, cEQ, AQ, BVAQ) and the functional connectivity of rSMG and rAG, second level group analyses implemented in SPM 12 were performed. The scores for each subscale as well as the total scores for the questionnaires were included as regressors in separate regression analyses.

## Results

### Behavioural results

As presented in the Supplementary Table 1 the mean scores for the questionnaires were consistent with the means previously reported for these questionnaires (Baron-Cohen et al., 2001; Bermond et al., 2007; Davis, 1980; Reniers et al., 2011). The only exception is the cEQ, where only the statistics for the total EQ score but not for the subscales were previously reported (Lawrence et al., 2004). Furthermore, none of the participants scored higher than 32 points on the total AQ scores, the cutoff score, which was associated with autism (Baron-Cohen et al., 2001). We also performed the analysis of the normality of the data, which showed that the data assessed by the IRI subscales (Empathic Concern, Perspective-taking, Fantasy) and a Peripheral Responsivity subscale of the QCAE were left skewed (see Supplementary Table 2). Moreover, the Perspective Taking (QCAE), Social Skill (AQ), Imagination (AQ), Emotionalizing (BVAQ), Fantasizing (BVAQ), Analyzing (BVAQ) and a total BVAQ measure were all right skewed (see Supplementary Table 2). The rest of the measures in the study were normally distributed (Supplementary Table 2).

### Seed regions related functional networks

As a first step, we separately analysed the functional connectivity of two seed regions: rSMG and rAG. The threshold for this analysis was set at $p < .05$ family-wise error rate correction (FWE) level with $k > 0$ (i.e. cluster extent > 0 voxel). This analysis revealed a positive connectivity pattern of the rSMG to the left SMG (lSMG), bilateral AI, right putamen, a cluster in the dACC/aMCC extending into the SMA, a cluster in the posterior MCC, extending into the superior parietal lobe, bilateral posterior MTG, extending into the posterior inferior temporal gyrus, a cluster encompassing the precentral gyrus (PrG) and the opercular part of the IFG, as well as clusters in the DLPFC (Figure 2, yellow-red areas). We also found decreased connectivity of the rSMG to the bilateral precuneus, bilateral AG, anterior and ventral mPFC, bilateral hippocampus, as well as the middle segment of the MTG and bilateral cluster in the superior frontal gyrus, corresponding to the BA 8 (Figure 2, blue-purple areas).

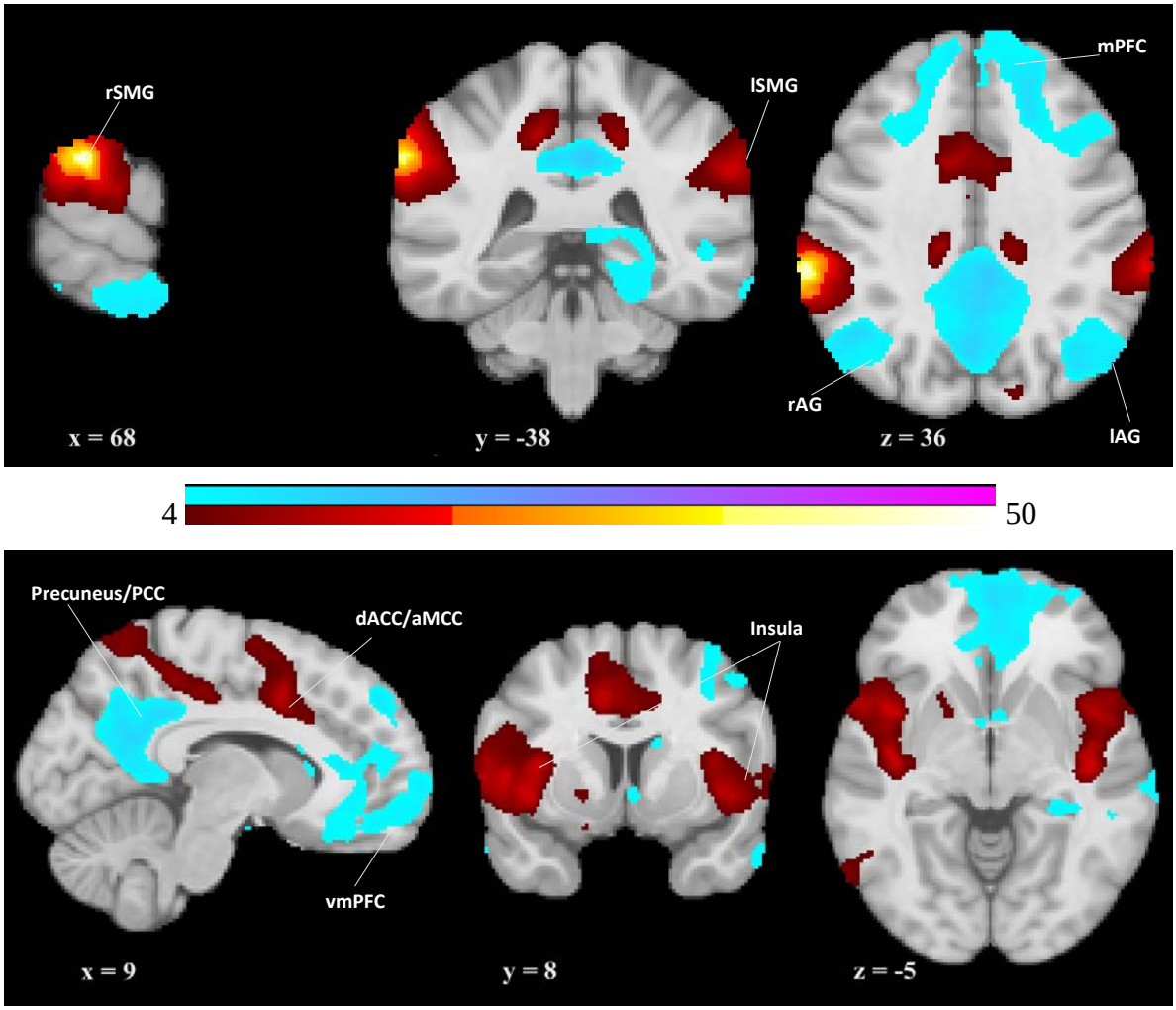


*Figure 2.* Results of the resting state connectivity analyses for rSMG. Yellow-red areas reflect positive connectivity pattern, blue-purple areas indicate decreased connectivity. aMCC = anterior midcingulate cortex; dACC = dorsal anterior cingulate cortex; lAG = left angular gyrus; lSMG = left supramarginal gyrus; rAG = right angular gyrus; rSMG = right supramarginal gyrus; PCC = posterior cingulate cortex; vmPFC = ventromedial prefrontal cortex. Own creation, 2018.

The connectivity analysis for the rAG seed regions revealed positive connectivity to the left AG (lAG) and a cluster in the posterior part of left STG, right precuneus, clusters in the right ventral and dorsal mPFC, triangular part of the rIFG, rMTG/rSTS, as well as the cluster, encompassing the posterior segment of the right middle frontal gyrus (rMFG) and medial segment of the right PrG (Figure 3, yellow-red areas). Further analysis revealed decreased connectivity of the rAG with bilateral SMG, left triangular part of IFG, left insula, right central operculum, a cluster in the right STG and transverse temporal gyrus, as well as the clusters in anterior lobe of cerebellum (Figure 3, blue-purple areas). It is important to note, that the identified clusters, which showed decreased connectivity with rAG were smaller.

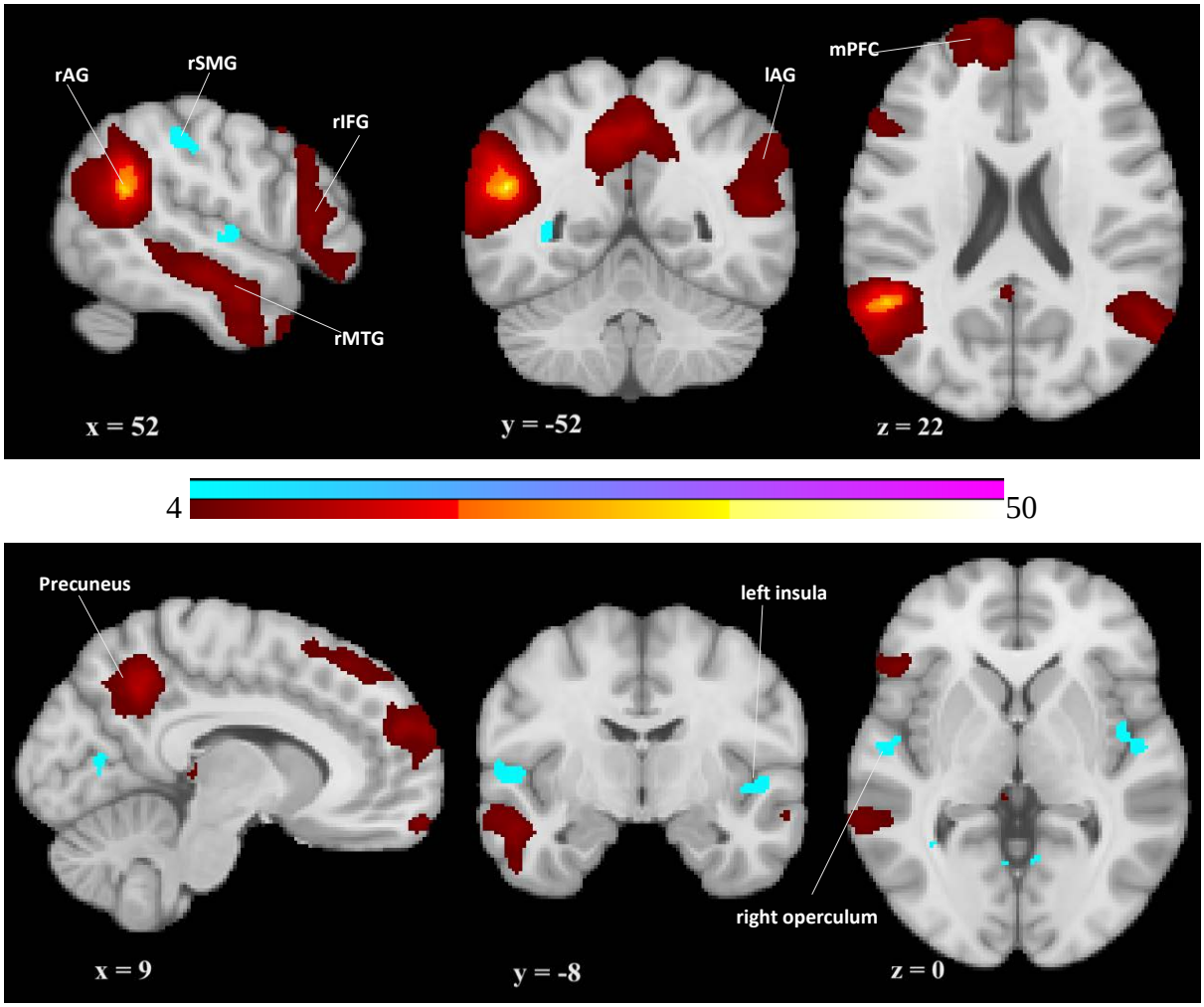


*Figure 3.* Results of the resting state connectivity analyses for rAG. Yellow-red areas reflect positive connectivity pattern, blue-purple areas indicate decreased connectivity. lAG = left angular gyrus; mPFC = medial prefrontal cortex; rAG = right angular gyrus; rIFG = right inferior frontal gyrus; rMTG = right middle temporal gyrus; rSMG = right supramarginal gyrus. Own creation, 2018.

**Personality traits related networks**

In order to investigate functional connectivity in association with affective and cognitive empathy traits assessed by self-reported questionnaires, we performed a separate regression analysis using each subscale of every questionnaire as well as the total measurement on the questionnaire as a covariate. The initial threshold for cluster defining was set $p < .001$. We then calculated the t-statistics with $p <. 05$ cluster-wise FWE correction. This analysis revealed nine significant clusters showing connectivity with rAG and eight significant clusters showing connectivity with rSMG.

**rSMG.** Our analysis revealed eight significant clusters, which showed personality traits specific modulations (Table 1).

Table 1

*rSMG functional connectivity related to the personality traits assessed by self-report questionnaires*

| Questionnaire Subscale | Region | MNI coordinates | | | Cluster level | | | Peak level | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | X | y | z | $P_{FWE-cor.}$ | $P_{uncor.}$ | $k_E$ | $P_{FWE-cor.}$ | $P_{uncor.}$ | $T$ |
| AQ social skills (+) | right middle/ posterior insula | 38 | -4 | 14 | 0.000 | 0.000 | 676 | 0.468 | 0.000 | 5.23 |
| AQ social skills (-) | bilateral thalamus | -4 | -2 | 8 | 0.000 | 0.000 | 1009 | 0.492 | 0.000 | 5.13 |
| | rIOG | 27 | -100 | 4 | 0.002 | 0.000 | 468 | 0.75 | 0.000 | 4.82 |
| BVAQ Identifying (+) | rMTG/ rTP | 51 | 4 | -26 | 0.032 | 0.001 | 289 | 0.376 | 0.000 | 5.28 |
| | rMOrG | 4 | 62 | -24 | 0.005 | 0.000 | 411 | 0.516 | 0.000 | 5.10 |
| IRI emotional concern (+) | bilateral LiG | 2 | -90 | -12 | 0.000 | 0.000 | 728 | 0.289 | 0.000 | 5.42 |
| | lMOG/ left occipital pole | -10 | -100 | 11 | 0.012 | 0.000 | 351 | 0.955 | 0.000 | 4.46 |
| IRI personal distress (-) | lMFG | -34 | 60 | 8 | 0.022 | 0.001 | 315 | 0.769 | 0.000 | 4.79 |

*Note:* MNI = Montreal Neurological Institute. $k_E$ = cluster size in voxels; $P_{FWE-cor.}$ = threshold corrected for family wise error; $P_{uncor.}$ = threshold uncorrected for multiple comparisons; T = t-statistics. AQ = Autism-Spectrum Quotient; BVAQ = Bermond-Vorst Alexithymia Questionnaire; IRI = Interpersonal Reactivity Index. (-) refers to negative correlation; (+) refers to positive correlation. LiG = lingual gyrus; lMFG = left middle frontal gyrus; lMOG = left middle occipital gyrus; rIOG = right inferior occipital gyrus; rMOrG = right medial orbital gyrus; rMTG = right middle temporal gyrus; rTP = right temporal pole.

Threshold p <.001.

We found stronger connectivity between rSMG and the cluster encompassing the right middle/posterior insula, the right central operculum and right postcentral gyrus, in participants with higher scores on the Social Skill subscale of AQ. An increased connectivity of rSMG with two clusters, including bilateral thalamus and left caudate, as well as the right inferior occipital

gyrus (rIOG), was found in participants with lower scores on this subscale. Thus, individuals with better social skills had stronger connectivity of rSMG with clusters encompassing bilateral thalamus (peak MNI: -4, -2, 8) and rIOG (peak MNI: 27, -100, 4; BA 18), and individuals with poorer social skills showed increased connectivity of rSMG with the cluster around the right insula (peak MNI: 38, -4, 14; BA 4).

We also found an increased connectivity between the rSMG with the cluster in the rMTG/rTP; peak MNI: 51, 4, -26; BA 38/21) and the cluster, encompassing the right medial orbital gyrus (rMOrG; peak MNI: 4, 62, -24; BA 11) and right gyrus rectus (or straight gyrus) for individuals, who scored high on the Identifying subscale of BVAQ, compared to those who scored lower. Higher scores on this subscale are indicative of higher proneness to alexithymia and are associated with more difficulties in identifying and differentiating individual's own emotional states.

Furthermore, individuals, who scored high on the Empathic Concern subscale of IRI showed greater connectivity of the rSMG with the cluster in the bilateral lingual gyrus (LiG; peak MNI: 2, -90, -12; BA 18), as well as with a cluster, encompassing the left occipital pole and the left middle occipital gyrus (lMOG; peak MNI: -10, -100, 11; BA 18). The connectivity between rSMG and the cluster in the left middle frontal gyrus (lMFG; peak MNI: -34, 60, 8; BA 10) was stronger for the participants with lower scores on the Personal Distress subscale of IRI. These results indicate that individuals with greater feelings of concern for other people showed greater connectivity of rSMG with two separate clusters in the visual cortex and visual association area. Moreover, individuals with less feelings of personal distress in social situations had greater connectivity between rSMG and the cluster in the lMFG.

**rAG.** The analysis revealed nine significant clusters, displayed in Table 2.

Table 2

*rAG functional connectivity related to the personality traits assessed by self-report questionnaires*

| Questionnaire/ Subscale | Region | MNI coordinates | | | Cluster level | | | Peak level | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | x | y | z | $P_{FWE-cor.}$ | $P_{uncor.}$ | $k_E$ | $P_{FWE-cor.}$ | $P_{uncorr.}$ | $T$ |
| AQ attention switching (-) | left precuneus | -4 | -56 | 50 | 0.039 | 0.001 | 295 | 0.293 | 0.000 | 5.38 |
| AQ Total (-) | rOpIFG/ rMFG | 40 | 16 | 28 | 0.000 | 0.000 | 757 | 0.092 | 0.000 | 5.91 |
| BVAQ fantasizing (-) | bilateral SMA | 0 | 14 | 50 | 0.041 | 0.002 | 292 | 0.869 | 0.000 | 4.61 |
| | rPrG/ rOpIFG | 52 | 8 | 16 | 0.000 | 0.000 | 644 | 0.870 | 0.000 | 4.61 |
| QCAE proximal responsivity (-) | lMTG/ lSTS | -45 | -24 | -13 | 0.000 | 0.000 | 660 | 0.300 | 0.000 | 5.36 |
| IRI personal distress (-) | posterior lAG | -39 | -60 | 40 | 0.002 | 0.000 | 518 | 0.347 | 0.000 | 5.29 |
| | posterior rAG | 39 | -60 | 58 | 0.024 | 0.001 | 332 | 0.574 | 0.000 | 4.99 |
| | lMFG | -38 | 29 | 32 | 0.002 | 0.000 | 526 | 0.731 | 0.000 | 4.80 |
| | rMFG | 32 | 29 | 28 | 0.013 | 0.000 | 379 | 0.822 | 0.000 | 4.68 |

*Note*. MNI = Montreal Neurological Institute. $k_E$ = cluster size in voxels; $P_{FWE-cor.}$ = threshold corrected for family wise error; $P_{uncor.}$ = threshold uncorrected for multiple comparisons; T = t-statistics; AQ = Autism-Spectrum Quotient; BVAQ = Bermond-Vorst Alexithymia Questionnaire; IRI = Interpersonal Reactivity Index; QCAE = Questionnaire of cognitive and affective empathy. (-) refers to negative correlation; (+) refers to positive correlation. lAG = left angular gyrus; lMFG = left middle frontal gyrus; lMTG = left middle temporal gyrus; lSTS = left superior temporal sulcus; rAG = right angular gyrus; rMFG = right middle frontal gyrus; rOpIFG = right opercular part of inferior frontal gyrus; rPrG = right precentral gyrus; SMA = supplementary motor area. Threshold p <.001.

We found an increased connectivity of the rAG with the left precuneus (peak MNI: -4, -56, 50; BA 7) in participants, who scored low on the Attention Switching subscale of the AQ, as well as a greater connectivity with the cluster (peak MNI: 40, 16, 28) including right opercular part of the IFG (rOpIFG) and rMFG, for participants who scored low on the total AQ scale. These results suggest that individuals with greater attention switching capacity show increased connectivity between rAG and left precuneus. Furthermore, individuals, who scored lower on the whole AQ questionnaire, and therefore showed less traits of autistic-like behaviour overall, had higher connectivity between rAG and the cluster comprising the rIFG and the rMFG, corresponding to the BA 9/BA 44.

Participants with lower scores on the Fantasizing subscale of the BVAQ showed stronger connectivity between rAG and two separate clusters, one including the bilateral supplementary motor cortex (SMA; peak MNI: 0, 14, 50; BA 6) and another one comprising the right precentral gyrus (rPrG) and the rOpIFG (peak MNI: 52, 8, 16; BA 44). Thus, the connectivity was stronger in participants, who had less difficulties to fantasize and imagine virtual matters.

Moreover, we found stronger connectivity within the rAG network with the left posterior AG (peak MNI: -39, -60, 40; BA 39) and more posterior segment of rAG (peak MNI: 39, -60, 58; BA 7), and the bilateral MFG (peak MNI: -38, 29, 32 and 32, 29, 28; BA 9), for the participants, who reported to experience less feelings of distress in social situations (scored low on the Personal Distress subscale of IRI).

We also found an increased connectivity of the rAG with the cluster in the lMTG/lSTS (peak MNI: -45, -24, -13; BA 21) in participants, who scored low on the Proximal Responsivity subscale of the QCAE. In other words, in individuals, who experience lower affective response to the mood of others, the connectivity between rAG and lMTG/lSTS was stronger.

## Discussion

The current thesis was conducted within a study, aiming to deepen the understanding of the mechanisms underlying the EEB in the emotional domain and to investigate the role of the rSMG in self-other distinction and in overcoming the EEB. Self-other distinction is suggested to be one of the key mechanisms in social cognition, which enables people to differentiate between the mental states of oneself and those of other people. A functioning self-other distinction mechanism is crucial for empathy and ToM, and is seen as a mechanism, which controls the shared representations and prevents people from making egocentric judgments (for a review see Lamm et al., 2016; Steinbeis, 2016). Neuroscientific research

focused on the investigation of the neural underpinnings of empathy and ToM and the underlying self-other-distinction mechanism demonstrated that one of the key brain regions associated with these processes, is rTPJ (for a review see Bukowski & Lamm, 2017).

The specific goal of this thesis was to examine the functional connectivity profiles of two subregions (rSMG and rAG) within the rTPJ – the brain region, which was widely investigated and discussed and was shown to be involved not only in social cognition, but also in attention and memory processes. In the first part of the analysis, I looked into the functional connectivity of rSMG and rAG in the resting brain and identified the connectivity profiles for both regions. The results of this analysis will be discussed and integrated into previous theoretical and experimental research in the following section.

The second goal of this thesis was an exploratory investigation of the potential modulations related to self-reported empathy, alexithymia and autistic-traits within identified connectivity networks. Based on previous research, indicating the involvement of the subregions of the rTPJ in the ongoing differentiation between self and others, which is crucial for empathy, I decided to examine the relationship between the trait empathy, assessed by self-report measures, and the resting state networks. Moreover, because of the empathy-related impairments in ASD and alexithymia, I also correlated the self-reported alexithymia and autistic-traits to the resting state networks of the rSMG and rAG. In the second part of the Discussion section, I will interpret the results of this exploratory analysis, as well as discuss the limitations of this thesis and future directions for the research.

**Functional connectivity of the rSMG and rAG**

Our first research question in this thesis was focused on the investigation of the connectivity patterns of the rSMG and rAG. Based on the literature research, I expected to find distinct connectivity patterns for both regions and our findings supported this assumption. Our analysis revealed positive connectivity of the rSMG with such regions as the bilateral insula, IFG and dACC/aMCC, associated with emotional processing, empathy for pain, self-awareness and saliency (for a review see Bernhardt & Singer, 2012), as well as with the prefrontal regions, such as DLPFC, involved in cognitive control and decision making (Greene et al., 2004; Miller, & Cohen 2001). Further analysis showed decreased connectivity with brain regions such as AG, precuneus, PCC and anterior and ventral mPFC, which are associated with mentalizing and memory (Mitchell, 2009), and are part of the default mode network (DMN), the network that is most functionally connected during resting state (Raichle et al., 2001; Raichle, 2015). Concerning the connectivity profile of the rAG, the opposite pattern was found: positive

connectivity with regions, associated with DMN, but with most of the regions lying in the right hemisphere, and decreased connectivity with the bilateral SMG and insula. It is important to mention, that identified clusters showing decreased connectivity with rAG were smaller, compared to all other clusters revealed in the analysis.

TPJ is a brain region, whose function is widely discussed in neuroscientific research. Because rTPJ was suggested to be involved in different processes, and especially in such processes as mentalizing and self-other distinction in the domain of social cognition, as well as in attention and memory processes, and in integration of sensory information and self-awareness, the questions about the relationship between these functions and whether subregions within the rTPJ subserve different functions or whether there is an overarching function of this brain region, are currently debated (for review see Bukowski & Lamm, 2017). Various meta-analytical and experimental studies addressed these questions but the findings do not allow one to answer the questions with certainty. On the one hand, studies found a spatial overlap in activation in the rTPJ during ToM and attentional tasks (even though on the peak level the activations for both tasks were distinct and activated clusters were extending in different directions), and concluded that higher social cognition processes can rely on the similar computational mechanisms as attentional processes, and therefore indicating the potential overarching function (Decety & Lamm, 2007; Mitchell, 2008). On the other hand, another study reported smaller and more peripheral overlap and distinct peak activations, concluding that even though the activated regions are close to each other, they are distinct, and therefore supporting the fractioning view (Scholz et al., 2009).

Other recent studies, which demonstrated segregation within the region of rTPJ may shed some light into the discussion of the function of this brain region. Caspers et al. (2006, 2008) demonstrated that cytoarchitectonically the SMG can be divided into five subregions (PF, PFcm, PFm, PFop, PFt) and the AG into two separate subregions (PGa, PGp), which were found to show some interindividual variability in volume and no significant differences between hemispheres. Furthermore, Uddin et al. (2010) demonstrated that two subregions within lAG (PGa, PGp) differ not only cytoarchitectonically (as described by Caspers et al., 2006), but also show distinct structural and functional connectivity patterns. Another study examined structural and functional connectivity of the TPJ region, and showed that this region can be divided into three subregions, with distinct connectivity patterns (Mars et al., 2012).The distinct connectivity patterns for lSMG and lAG were also previously demonstrated (Cohen et al., 2008). Overall, these studies provide evidence that TPJ is not a homogeneous region, but shows structural and functional subdivisions.

Our findings from the functional connectivity analysis are in line with previous research, showing that two subregions, namely rSMG and rAG, have distinct connectivity profiles. The coordinates for rSMG (peak MNI: 68, -38, 36) were a priori defined based on the study from Silani et al. (2013). Even though on the peak level, coordinates in this analysis slightly differ and lie more on the surface and more superior, comparing to the coordinates (TPJa, peak MNI: 59, -37, 30) reported by Mars et al., (2012), the revealed connectivity pattern was similar, with the positive connectivity to the lSMG, prefrontal regions and insula. The coordinates for the rAG (peak MNI: 52, -52, 22) were also a priori defined and taken from the Silani et al. (2013) study, which reported them as peak coordinates for ToM based on the meta-analysis from Mar (2011). This region corresponds to the TPJp (peak MNI: 54, -55, 26; Mars et al., 2012) and shows similar connectivity profile with increased connectivity to lAG, precuneus, PCC and mPFC.

Furthermore, the connectivity patterns revealed in our analysis are similar to those revealed in the studies, which investigated the role of rTPJ in attention and social cognition by combined the meta-analytical approach to define the seed regions and analyzing the functional connectivity of these subregions. Based on meta-analysis in these studies that was divided into the anterior subregion, encompassing the rSMG, and associated with attentional processes, and posterior subregion, encompassing rAG and associated with ToM (Bzdok et al., 2013; Krall et al., 2015; Kubit & Jack, 2013). Additionally, Kubit and Jack (2013), identified the region with the center of gravity in between the rAG and rSMG, which was associated with attention reorienting, while rSMG was suggested to be involved in a different attentional task, namely target detection. The functional connectivity analysis in these studies showed similar connectivity patterns for aTPJ (positive connectivity with AI, IFG, ACC/MCC, premotor cortex and SMA) and for pTPJ (positive connectivity with precuneus, PCC, mPFC and posterior TPJ regions) (Bzdok et al., 2013; Krall et al., 2015; Kubit & Jack, 2013). Furthermore, decreased connectivity of these two subregions (aTPJ showed decreased connectivity with pTPJ, precuneus, PCC and mPFC, while pTPJ was negatively correlated with AI, SMG/IPS and IFG) suggest that these subregions belong to two distinct antagonistic networks (Bzdok et al., 2013; Kubit & Jack, 2013). Even though our findings overall are consistent with those described before, it is important to note that seed regions for the rsfMRI in these studies lie more ventral compared to the seed regions used in our analysis. Further comparison of the connectivity profiles in our analysis and those in two recent studies, which used very similar seed regions, revealed identical connectivity patterns (Hoffmann et al., 2016; Steinbeis et al., 2015). Finally, in order to directly compare our resting state analysis results I used a meta-

analytical database Neurosynth (https://www.neurosynth.org, 2018), which provides functional connectivity and meta-analytic coactivation maps related to a given region of interest based on the meta-analysis of 11406 studies (April, 2018). Visual comparison of the connectivity patterns showed matching connectivity networks. The inspection of terms, associated with the activations in each region (see Supplementary Table 3), demonstrated that both regions are associated with different psychological terms and brain regions.

In recent years several models describing the potential overarching function of the rTPJ were proposed. The fact, that rTPJ can be divided into subregions, with distinct connectivity patterns, does not automatically prove that the fractioning view is correct. It can fit the overarching view as well, with the notion that different subregions mediate the same function or processes but in different domains (Cabeza et al., 2012). Some approaches explained the involvement of the rTPJ in attention and social cognition by giving it the function of attention shifting and perspective shifting (Corbetta et al., 2002, 2008). rTPJ was shown to be a part of the ventral attention network, which is involved in the detection of salient stimuli and reorienting attention to them, and therefore has the function of a "circuit breaker" for the dorsal attentional network (internally oriented, goal-driven), when salient or unexpected stimuli appear (Corbetta et al., 2002, 2008). In the domain of social cognition the function of the rTPJ can be explained by the same mechanism of reorienting or shifting of perspective (Corbetta et al., 2008). Furthermore, because rTPJ was shown to be critically involved in self-awareness and integration of multisensory information (Blanke & Arzy, 2005), there is an assumption, that its function is to switch between internally driven networks and self-perspective and externally driven networks and the other's perspective (Corbetta et al., 2008). More recent functional connectivity studies, which were mentioned previously and demonstrated distinct connectivity patterns of the subregions within rTPJ attribute this overarching reorienting or "circuit breaking" function to the aTPJ (including rSMG) (Krall et al., 2015; Kubit & Jack, 2013). Moreover, findings from a recent TMS study are in line with this assumption of the overarching function of the aTPJ, which was shown to be involved in both, attentional and ToM tasks (Krall et al., 2016).

There are also other models, which aim to explain the function rTPJ and its involvement in various cognitive processes. On the one hand, Carter and Huettel (2013) suggested the integrative role of TPJ and formulated a nexus model, in which the main function of TPJ is to integrate information coming from different streams (attention, memory, bodily sensations, language, etc.) and to provide a social context for further decision making processes. According to this view, subregions such as SMG, AG, or STS subserve distinct processes, but in the TPJ

these streams converge together, producing a new integrative function of the TPJ (Carter & Huettel, 2013). Another model was formulated by Geng and Vossel (2013) and proposed that the function of the TPJ is contextual updating. In this model TPJ plays a crucial role in comparing the internal models about the environment or other people, to external events, and in updating these models accordingly. The authors also notice that various subregions might mediate a similar model updating function, but in different domains (Geng & Vossel, 2013). A similar account but with the main focus on the AG was proposed by Seghier (2013), which suggested an integrative role of the AG. According to this model the AG integrates multimodal information, generates the internal representations and compares these to the predictions coming from higher levels. In case the internal representation and the prediction do not match, the generated difference (so called "prediction error") is sent forward in order to change and update the prediction (Seghier, 2013).

In summary, previously discussed studies demonstrated that TPJ is a region, which is involved in various processes and consists of several subregions with distinct connectivity patterns. There are various models, aiming to explain the underlying computational processes and a potential overarching function of this region, but further studies are needed to deepen that understanding. The fact that not only subregions within TPJ, such as SMG and AG, showed distinct connectivity patterns, but also the further subdivisions within the AG, were reported to have some differences in functional connectivity (Uddin et al., 2010), demonstrate the necessity of further research in this area. As it was mentioned before, five cytoarhitectonical subdivisions within SMG were found (Caspers et al., 2006, 2008), further research of the connectivity patterns of these subdivisions should be informative and shed some light into the discussion of the function of this region.

**Self-report measures related modulations in resting state networks**

The second research question of this thesis addressed the exploratory investigation of the relationships between trait empathy, as well as alexithymia and autistic traits, assessed by self-report instruments, and the rSMG and rAG networks. The self-report data, displaying different aspects of empathy, alexithymia and autistic behaviour, were separately correlated with the resting state networks of the rSMG and rAG, in order to explore potential trait related modulations within these networks. Because previous studies demonstrated that the region of rTPJ is critically involved in empathy and self-other distinction, and rSMG specifically was shown to play a crucial role in the self-other distinction in the emotional domain, three questionnaires (IRI, QCAE, cEQ) assessing empathy and its aspects, were included in this

analysis (for a review see Lamm et al., 2016; Steinbeis, 2016). Furthermore, altered functioning in several brain regions, including rTPJ, was previously associated with deficits characteristic to the ASD and alexithymia (for a review see Bird & Cook, 2013; Frith, 2001; Lamm et al., 2015). So, two self-report instruments (BVAQ, AQ), which assess the dimensions of alexithymia and autistic traits, were applied, and these data were correlated to the resting state networks. Overall, our analysis revealed 17 regions, whose resting state connectivity with the rSMG or rAG was significantly associated with individuals scores of empathy, alexithymia, or autism (see Table 1, p. 30, and Table 2, p. 32). For each of these revealed regions the analysis of the associated terms was performed using the Neurosynth database (https://www.neurosynth.org, 2018). According to this neuroimaging meta-analytic database, which extracts the content from abstracts of thousands of neuroimaging studies and the reported peak coordinates, the peak locations of the clusters revealed in our analysis, showing connectivity with the rSMG and rAG, were associated with the functional terms presented in Supplementary Table 4 and Supplementary Table 5, respectively.

Firstly, the trait empathy related modulations in both networks were identified. The analysis revealed, that individuals, who showed lower affective response to the mood of others, measured by the Proximal Responsivity subscale of QCAE, had increased connectivity of the rAG with the cluster in the lMTG (peak MNI: -45, -24, -13; BA 21). This subscale belongs to the affective empathy component, and its items (*"I often get emotionally involved with my friends' problems"*, *"Friends talk to me about their problems as they say that I am very understanding"*, etc.) measure the affective response to the states of others in social situations (Reniers et al., 2011). The revealed cluster is situated in the medial segment of the lMTG, encompassing a segment of lSTS, corresponds to the BA 21. This brain region is a part of the DMN, whose activity is associated with the resting brain, mind-wandering and self-referential thoughts (for a review see Raichle, 2015). Furthermore, lSTS is associated with processing of speech, comprehension and semantic processing, as well as auditory processing (Bukowski & Lamm, 2018). Interestingly, a recent study reported an activation of a similar cluster in the lMTG and suggested that both, TPJ and MTG, are involved not only in cognitive mentalizing (or attribution of beliefs), but are also involved in affective mentalizing (attribution of emotions) (Corradi-Dell'Acqua, Hofstetter, & Vuilleumier, 2014). Also, Schulte-Rüther et al. (2008) reported activations in the lMTG during evaluation of the emotional states of others. Thus, both rAG and lMTG/lSTS are a part of the DMN and are associated with social cognition and such processes as the attribution and evaluation of mental states and self-other distinction. Therefore, on the one hand, the increased connectivity between rAG and lMTG in the

participants who reported a less affective response to the states of others, can be indicative of better differentiation between one's own mental states and those of others and better attribution of mental states to others. On the other hand, the self-other distinction in the emotional domain was previously associated with the involvement of the rSMG, while rAG was assumed to subserve this function in the cognitive domain (for a review see Steinbeis, 2016). Considering that rSMG was found to be involved in overcoming the EEB (Silani et al., 2013) and that it was also associated with the attribution and evaluation of emotions and pain (Corradi-Dell'Acqua et al., 2014), it is possible that rSMG is involved in the self-other distinction but in the affective domain, which cannot be assessed by the questionnaires. Therefore, it is possible that the revealed connectivity pattern reflects the more cognitive approach of the emotion understanding and attribution.

Furthermore, the trait empathy specific modulations in the rSMG network were found. Individuals, who reported greater feelings of empathic concern, assessed by the Empathic Concern subscale of IRI, had increased connectivity between the rSMG and two clusters in the visual cortex. This subscale is related to the affective empathy component and measures the feelings of concern and compassion toward other people with following items: "*Other people's misfortunes do not usually disturb me a great deal*", "*I am often quite touched by things that I see happen*", "*When I see someone being treated unfairly, I sometimes don't feel very much pity for them*", etc. (Davis, 1980). The first identified cluster (peak MNI: 2, -90, -12; BA 18), extending from the posterior end of LiG into the anterior part and further into a calcarine cortex. The second cluster (peak MNI: -10, -100, 11; BA 18) identified in our analysis extends from the left occipital pole into the lMOG and left superior occipital gyrus. These revealed clusters are located in the occipital lobe and are a part of the visual and the visual association cortices, which are associated with visual processing. In a recent study, the LiG was reported as one of the brain regions, which was more activated during observation of scenes with live actors than in scenes with animated characters (Mar, Kelley, Heatherton, & Macrae, 2007). Mar et al. (2007) explained these findings through the sensitivity of the LiG to the characteristics of the stimuli depicting the live actions, previously described by Backus, Fleet, Parker, & Heeger, 2001. Furthermore, some studies also reported activations in the LiG and MOG in association with the perception and identification of facial expressions (Kitada, Johnsrude, Kochiyama, & Lederman, 2010; Pavuluri, O'Connor, Harral, & Sweeny, 2007). Previously, Silani et al. (2013) also reported an interaction between rSMG and somatosensory and visual areas (though more lateral and anterior comparing to the clusters revealed in our analysis) in the situation of a mismatch between one's own and another person's experiences, and explained this relationship

by the role of rSMG in the integration of multisensory information concerning oneself and others. Because empathic concern assesses the other-oriented feelings induced in social situations, and requires the distinction between one's own feelings and those of others, the increased connectivity between occipital regions and rSMG might be explained by a similar mechanism of information integration. Furthermore, because inferring the emotions of others relies on visual information, the increased connectivity with the visual areas might reflect the importance of this sensory information while taking perspective of others and understanding their emotions.

Moreover, people, who reported experiencing less personal distress in social situations, had greater connectivity between rSMG and a cluster in the left anterior PFC extending into lDLPFC (peak MNI: -34, 60, 8; BA 10). Also people experiencing less personal distress, showed increased connectivity of the rAG and clusters in bilateral IPL (peak MNI: 39, -60, 58, BA 7; -39, -60, 40, BA 39) and bilateral DLPFC (peak MNI: 32, 29, 28; -38, 29, 32; BA 9). The personal distress is related to the feeling of anxiety and discomfort in social situations and was obtained by the Personal Distress subscale of IRI, comprising such items as: "*When I see someone who badly needs help in an emergency, I go to pieces*" "*I sometimes feel helpless when I am in the middle of a very emotional situation*" "*I tend to lose control during emergencies*", etc. (Davis, 1980). These revealed connectivity patterns are interesting, because it was previously suggested that both rSMG and rAG play a role in self-other distinction in the emotional and cognitive domain. Personal distress can be indicative of a dysfunctional self-other distinction mechanism, due to this dysfunction people adopt the affective states of others, which leads to discomfort, distress and aversive behaviour (Singer & Lamm, 2009). Therefore, people who have a better differentiation between the state of oneself and those of others, might experience less feelings of anxiety and distress. A recent study demonstrated that stronger connectivity between rSMG and lDLPFC resulted in a smaller EEB, suggesting the role of rSMG in self-other distinction and later involvement of lDLPFC in decision making or making a judgment about the feelings of another person (Steinbeis et al., 2015). Thus, our findings of trait specific modulations in the connectivity between rSMG and a cluster in the left anterior PFC/lDLPFC are in line with previous research. Also, Moriguchi et al. (2007) reported activations in the similar region and emphasized the role of DLPFC in the regulatory and evaluating function when judging others pain. Previous studies proposed TPJ and mPFC as typical regions involved in the ToM (Gallagher & Frith, 2003). Our analysis revealed the increased connectivity between rAG and clusters in the bilateral DLPFC in people experiencing less personal distress, probably due to better self-other distinction. Lesion studies previously

suggested that impairments in cognitive aspects of the ToM can be associated with lesions, encompassing not only ventral mPFC but also DLPFC (Shamay-Tsoory & Aharon-Peretz, 2007). In general, there are different assumptions about the role of the various frontal regions in mentalizing about others, such as a general executive control function, perspective selection, inhibition of self-perspective (for a review see Samson, Apperly, Kathirgamanathan, & Humphreys, 2005). Further studies, combining task and questionnaire data, examining the relationships between temporal and frontal regions and modulations within networks, are necessary.

Even though, our sample consisted of healthy participants, I also examined autistic and alexithymia trait related modulations within rSMG and rAG networks. The AQ, measures the degree to which individuals have autistic traits. Findings showed that individuals, who reported better attention switching ability on the AQ, had greater connectivity of the rAG and left precuneus (peak MNI: -4, -56, 50; BA 7). Attention switching was assessed by such items as: "*I frequently get so strongly absorbed in one thing that I lose sight of other things*", "*I find it easy to do more than one thing at once*", etc. (Baron-Cohen et al., 2001). The precuneus was shown to be involved in various processes, as for example, episodic memory retrieval, self-consciousness, first- and third-person perspective taking, mental imagery, motor coordination and visuospatial direction of attention (for a review see Cavanna & Trimble, 2006). Both rAG and precuneus were associated with the DMN, although some scholars argued that precuneus might not be a part of the DMN (for a review see Raichle, 2015; Raichle et al., 2001; Zhang & Li, 2012). The DMN was previously suggested to be anticorrelated with dorsal attentional network, which is involved in the reorienting of attention to the new relevant stimuli (Fox et al., 2005). While an earlier study proposed that rTPJ is involved in reorienting attention (Corbetta et al., 2002), more recent studies suggested that specific subregions within rTPJ, can be associated with internally and externally oriented attention (Bzdok et al., 2013). It was also suggested that precuneus might not only be a central node within DMN, but that it is also interacting with attentional networks (Utevsky, Smith, & Huettel, 2014). A recent study examining the functional connectivity and functions of the subregions within a posterior medial cortex, showed that precuneus is a subregion, which can be involved in the shifting of attention (Bzdok et al., 2015). Also, Zhang and Li (2012) demonstrated that ventral and dorsal parts of precuneus have distinct connectivity and are associated with different processes. While ventral precuneus can be associated with DMN and is involved in memory retrieval, self-processing and empathy, the dorsal precuneus was associated with mental imagery and visuospatial attention (Zhang & Li, 2012).

Furthermore, people, who showed less autistic-like traits overall (assessed by the AQ), had increased connectivity of the rAG and a cluster comprising rIFG and rMFG, corresponding to the BA 9 and BA 44. These findings are interesting because the region of the rIFG was previously shown to be a part of the MNS and was often associated with emotion recognition and empathy (Schulte-Rüther et al., 2007; Shamay-Tsoory et al., 2009). The IFG was also demonstrated to play an important role in the ToM and self-perspective inhibition (Samson et al., 2005). Moreover, studies associated ASD related deficits with impaired ToM and cognitive empathy (for a review Frith, 2001; Frith & Happe, 2005). So, one potential interpretation of these connectivity results, is that people with stronger connectivity between rAG and IFG, which are associated with self-other distinction and inhibition of self-perspective, can better differentiate between oneself and others, take perspective of other people and therefore show less autistic traits.

The AQ subscale named Social Skill is comprised of the following items: "*I prefer to do things with others rather than on my own*", "*I find it easy to work out what someone is thinking or feeling just by looking at their face*", "*I find it difficult to work out people's intentions*", etc. (Baron-Cohen et al., 2001). Social skills include a wide range of different abilities (gaze following, face recognition, imitation, joint attention, mentalizing and perspective-taking, etc.), which develop gradually and enable one to interact with others and manage social situations (for a review see Happe & Frith, 2014; Soto-Icaza, Aboitiz, & Billeke, 2015). In the current study people, who reported to have better social skills had stronger connectivity of rSMG and a cluster encompassing the thalamus and extending into the left caudate (peak MNI: -4, -2, 8), and a cluster in the visual association area (peak MNI: 27, -100, 4; BA 18). The thalamus is a region, which is divided into several nuclei, has bidirectional connections with the cortex and was associated with multiple functions, such as integration and the relay of sensory and motor information, pain processing, state of alert and consciousness (White & Alkire, 2003; Behrens et al., 2003). Based on the thalamic subdivisions described in the recent study of Battistella et al. (2017), the cluster revealed in our analysis, corresponds to the bilateral anterior segment and left mediodorsal segment of thalamus, which are connected with the limbic structures and the frontal cortex. Furthermore, people with poorer social skills showed stronger connectivity between rSMG and a cluster in the right hemisphere (peak MNI: 38, -4, 14; BA 4), encompassing the right posterior insula and central operculum, and extending into primary motor and somatosensory areas. The posterior insula is a region, which was previously found to be functionally connected with somatosensory and motor cortices, and also showed connectivity to the more posterior regions of ACC/MCC and was suggested to play a

crucial role in interoception (Craig, 2002; Deen, Pitskel, & Pelphrey, 2011; zu Eulenburg, Baumgaertner, Treede, & Dietrich, 2013).

In general, deficits associated with ASD were widely discussed in neuroscientific and clinical research. These deficits lie in different domains and the underlying mechanisms for each of them might be different (for a review see Happe, Ronald, & Plomin, 2006). Autism is a disorder, which was related to the atypical connectivity. On the one hand a hypothesis of underconnectivity in ASD was proposed and stated that cortical regions show general reduced connectivity (Castelli et al., 2002; Just et al., 2004). On the other hand, other studies investigating the connectivity between cortical and subcortical structures suggested an increased thalamicocortical connectivity (Mizuno et al., 2006; Tomasi & Volkow, 2017). Thus, despite the current debate on the exact neural mechanisms underlying ASD, the atypical connectivity (under- and overconnectivity) of various brain regions can be associated with different ASD symptoms and its severity (for a review see Hull et al., 2017; Kana, Uddin, Kenet, Chungani, & Müller, 2014). The results of our connectivity analysis can add further information in this field of research and be useful for future studies, examining the autistic trait related modulations in resting state networks.

Finally, our analysis revealed increased connectivity of the rSMG and a cluster in the anterior rMTG/rTP (peak MNI: 51, 4, -26; BA 38/21) and a cluster in the OFC (peak MNI: 4, 62, -24; BA 11) in individuals, who reported more difficulties in identifying and differentiating emotions. This ability was assessed by the Identifying subscale of the BVAQ, which contains such items as: "*When I am distressed, I know whether I am afraid or sad or angry*", "*When I am fed-up, it remains unclear to me whether I am sad or afraid or unhappy*", etc. (Vorst & Bermond, 2001). As it was mentioned before both regions were previously associated with the ToM. The involvement of the OFC, and vmPFC more specifically, was associated with understanding the affective states of others and self-referential thoughts (Mitchell et al., 2006; Shamay-Tsoory & Aharon-Peretz, 2007; Shamay-Tsoory et al., 2009). OFC is interconnected with limbic structures and more ventral parts of the OFC were shown be to be involved in reward learning, motivational evaluation and affective decision-making (for a review see Happaney, Zelazo, & Stuss, 2004; Rudebeck, Bannerman, & Rushworth, 2008). The anterior temporal regions, encompassing the TP, were shown to be connected with medial frontal regions and OFC, as well as with limbic structures, and were associated with episodic memory (rTP) and semantic memory (lTP) and mentalizing (for a review see Bukowski & Lamm, 2017; Olson et al., 2007). The neural mechanisms underlying alexithymia are not fully understood and the findings are mixed. The impaired emotional processing and unawareness of emotional

states in alexithymia were previously linked to the dysfunction of the ACC and AI (for a review see Bird & Viding, 2014; Kano & Fukudo, 2013). There is also evidence of decreased activations in the OFC during emotion recognition tasks and in the vmPFC, associated with affective decision making, in alexithymia (Kano & Fukudo, 2013).

Another subscale of the alexithymia questionnaire (BVAQ) measures the fantasizing abilities and comprises following items: "*Before I fall asleep, I make up all kinds of events, encounters and conversations*", "*I like to think up bizarre imaginative stories*", etc. (Vorst & Bermond, 2001). Our analysis revealed stronger connectivity of the rAG and a cluster in the SMA (peak MNI: 0, 14, 50; BA 6), as well as with a cluster, encompassing rPrG and the rOpIFG (peak MNI: 52, 8, 16; BA 44), in individuals who reported higher fantasizing abilities. As previously mentioned, the region of rIFG is considered to be a part of the MNS and was associated with emotion recognition and affective empathy, imitation as well as with self-perspective inhibition (Samson et al., 2005; Shamay-Tsoory et al., 2009). In the motor domain, the dorsal OpIFG was found to be involved in both, action observation and imitation, indicating that this area is a core region of the MNS (Molnar-Szakacs, Iacoboni, Koski, & Mazziotta, 2005). Furthermore, SMA was associated with movement control, preparing and planning of movement and action sequences, as well as with the cognitive control and inhibition of subconsciously evoked movements (for a review see Nachev, Kennard, & Husain, 2008). Concerning the associations between these regions and alexithymia, there is some evidence of increased sensitivity of the MNS and activation of premotor areas in individuals with alexithymia (for a review see Moriguchi & Komaki, 2013). The impairments in fantasizing in alexithymia are associated with poorer, less emotional and intense imagery, and were previously related to the reduced activation in the PCC (Mantani, Okamoto, Shirao, Okada, & Yamawaki, 2005).

The alexithymia traits related modulations identified in our analysis are difficult to interpret, considering quite mixed findings in the past and the fact that no comparison between different groups with various degrees of alexithymia and healthy controls was performed. But our findings demonstrated that there might be some specific modulations in the resting states networks associated with proneness to alexithymia, and further research combining experimental paradigms and questionnaire data, and comparing different groups might contribute to a better understanding of the mechanisms underlying alexithymia.

**Limitations**

The current thesis has several limitations, which should be discussed and taken into account in future research. First of all, our sample consisted only of female participants, which makes it impossible to generalize our result into the whole population. Moreover, most of the participants were of a young age and were students. Future studies should address these issues, and test different samples, and considering the results of an exploratory analysis, also compare healthy and clinical groups.

Further limitations in the current thesis are related to the use of self-report instruments. According to our procedure, participants filled out the questionnaires online a few weeks before they were invited to the testing session. On the one hand, this results in a lack of control of the conditions in which participants were filling out the questionnaires. On the other hand, the completion of the questionnaires via email might have made participants feel more anonymous and therefore reduces social desirability bias. Another issue, which should be addressed, is the low Cronbach's alpha coefficient for the subscales of AQ and Proximal Responsivity and Emotional Contagion subscales of QCAE. Although, as it was mentioned in the Method (p. 22, 25) these questionnaires were previously well-validated and the internal consistency coefficient tends to be low in small samples and with subscales comprised of few items, future studies should take this into account when considering the results of our exploratory analysis. Also the fact that some measures were exposed to the left- or right-skewed distribution, should be noted. Furthermore, the use of self-report questionnaires when assessing alexithymia is often critically discussed in the research and should be taken into consideration in future studies, testing alexithymic groups (Mueller, Buehner, & Ellgring, 2004).

According to our study design, the resting state acquisition followed the first testing block, which might have had an effect on the resting state data (Power, Fair, Schlaggar, & Petersen, 2010; Yeo et al., 2011). Although, our findings are in line with previous research on connectivity of the rSMG and rAG, it might be informative to compare the connectivity profile between the two testing sessions, as well as to compare resting state connectivity obtained before and after the experimental task. Another limitation, concerns potential effects of the physiological state of participants, such as sleepiness. Even though participants were instructed to concentrate on the fixation cross presented in the middle of the screen, the resting state acquisition was performed in the end of the first testing session. No additional control measures, such as eye-tracking, during the data acquisition were applied, but according to the feedback questionnaire participants did not report to have fallen asleep while being in the scanner.

In general, one of the limitations in the studies investigating the segregation within rTPJ and the functional connectivity of its subregions, is the definition of the borders of these subregions. Because of the difference of approaches in ROI definition, these studies are not easily comparable. Furthermore, in the current thesis the seed regions were a-priori defined, which can be considered a limitation. Because of the individual anatomical variability of the rTPJ, future studies should consider defining the seed regions for the connectivity analysis from the experimental task, performed by the same participants. Moreover, TPJ is considered to integrate multisensory information and is critically involved in various processes, so the analysis of the co-activation of the subregions within TPJ with other brain regions during certain tasks, can be informative in the current debate of the function of TPJ (Mitchell, 2008; Seghier, 2013).

**Summary and conclusion**

The neural mechanisms underlying our ability to understand others mental states were widely investigated and discussed in the past years. Various studies using different research methods were undertaken and several regions and networks, underlying the processes of social cognition were described. One of the regions, whose function was considered to be crucial not only in social cognition, but also in non-social processes, is the rTPJ. The goal of this thesis was to further investigate the function of this region and its subregions, and more specifically look into the functional connectivity of its subregions. Our findings are in line with previous research, and demonstrate that subregions within rTPJ show distinct connectivity profiles and might mediate similar functions but in different domains. Up to this date there is no unified theory on the function of the rTPJ, and further research, combining different methods and paradigms, is necessary to identify the potential overarching function of this region.

Furthermore, an exploratory analysis demonstrated the empathy trait related modulations in the resting state networks. Also the autistic and alexithymia traits related modulations in the resting state networks were identified. These results can contribute to the further understanding of these disorders and be especially useful for clinical research. Thus, in the future it might be possible to identify certain specific modulations linked to the personality traits, which can indicate a presence or a tendency toward certain clinical conditions. Further understanding of exact mechanisms underlying such disorders as ASD and alexithymia, are crucial for successful development and improvement of treatment and therapy approaches.

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**List of abbreviations**

| | |
|---|---|
| AC-PC | anterior commissure - posterior commissure |
| ACC | anterior cingulate cortex |
| AFNI | Analysis of Functional Neuroimages |
| AG | angular gyrus |
| AI | anterior insula |
| aMCC | anterior midcingulate cortex |
| ANT | Advanced Normalization Tools |
| APA | American Psychiatric Association |
| AQ | Autism Quotient |
| AS | Asperger Syndrome |
| ASD | Autism Spectrum Disorder |
| BA | Brodmann area |
| BOLD | blood oxygen level dependent |
| BVAQ | Bermond-Vorst Alexithymia Questionnaire |
| cEQ | Cognitive Empathy Quotient |
| cTBS | continuous theta burst stimulation |
| dACC | dorsal anterior cingulate cortex |
| DMN | default mode network |
| DLPFC | dorsolateral prefrontal cortex |
| DSM | Diagnostic and Statistical Manual of Mental Disorders |
| DTI | diffusion tensor imaging |
| EEB | emotional egocentricity bias |
| EPI | echo-planar imaging |
| EQ | Empathy Quotient |
| FFT | Fast Fourier Transform |
| fMRI | functional magnetic resonance imaging |
| FWE | family-wise error |
| FWHM | full-width at half-maximum |
| HFA | High Functioning Autism |
| IFG | inferior frontal gyrus |
| IPL | intraparietal lobe |
| IRI | Interpersonal Reactivity Index |
| lAG | left angular gyrus |

| | |
|---|---|
| LiG | lingual gyrus |
| lMFG | left middle frontal gyrus |
| lMOG | left middle occipital gyrus |
| lMOrG | left medial orbital gyrus |
| lMTG | left middle temporal gyrus |
| lOP | left occipital gyrus |
| lSMG | left supramarginal gyrus |
| lSTS | left superior temporal sulcus |
| lTP | left temporal pole |
| lTPJ | left temporoparietal junction |
| MCC | midcingulate gyrus |
| MFG | middle frontal gyrus |
| MNI | Montreal Neurological Institute |
| MNS | mirror neuron system |
| MOG | middle occipital gyrus |
| mOFC | medial orbitofrontal cortex |
| mPFC | medial prefrontal cortex |
| MTG | middle temporal gyrus |
| MRI | magnetic resonance imaging |
| OFC | orbitofrontal cortex |
| PANAS | Positive and Negative Affect Schedule |
| PFC | prefrontal cortex |
| PCC | posterior cingulate cortex |
| pMCC | posterior midcingulate cortex |
| pMTG | posterior middle temporal gyrus |
| PrG | precentral gyrus |
| QCAE | Questionnaire Cognitive and Affective Empathy |
| rAG | right angular gyrus |
| rIOG | right inferior occipital gyrus |
| rMOrG | right medial orbital gyrus |
| rMTG | middle temporal gyrus |
| rOFC | right orbitofrontal cortex |
| rOpIFG | right opercular part of inferior frontal gyrus |
| rsfMRI | resting state functional magnetic resonance imaging |

| | |
|---|---|
| rSMG | right supramarginal gyrus |
| rTMS | repetitive transcranial magnetic simulation |
| rTP | right temporal pole |
| rTPJ | right temporoparietal junction |
| SMA | supplementary motor area |
| SPM | Statistical Parametric Mapping |
| STG | superior temporal gyrus |
| STS | superior temporal sulcus |
| TE | echo time |
| TMS | transcranial magnetic stimulation |
| ToM | theory of mind |
| TP | temporal pole |
| TPJ | temporoparietal junction |
| TPJa/aTPJ | anterior temporoparietal junction |
| TPJp/pTPJ | posterior temporoparietal junction |
| TR | repetition time |
| vmPFC | ventromedial prefrontal cortex |

## Supplementary materials

### Supplementary Table 1

*Descriptive statistics for each subscale and questionnaire for all subjects*

| Subscale | Min. | Max. | Mean | SD | Variance |
|---|---|---|---|---|---|
| **IRI** | | | | | |
| Empathic concern | 6.00 | 28.00 | 21.18 | 4.70 | 22.10 |
| Personal distress | 4.00 | 21.00 | 13.47 | 4.40 | 19.35 |
| Perspective-taking | 6.00 | 26.00 | 20.18 | 4.32 | 18.64 |
| Fantasy | 2.00 | 28.00 | 19.79 | 6.41 | 41.19 |
| **EQ** | | | | | |
| cEQ | 8 | 22 | 13.26 | 3.87 | 14.99 |
| **QCAE** | | | | | |
| Perspective taking | 26.00 | 40.00 | 31.38 | 3.33 | 11.09 |
| Online simulation | 18.00 | 35.00 | 28.12 | 3.85 | 14.83 |
| Emotion contagion | 8.00 | 15.00 | 11.59 | 1.54 | 2.37 |
| Proximal responsivity | 10.00 | 16.00 | 12.29 | 1.51 | 2.28 |
| Peripheral responsivity | 6.00 | 16.00 | 12.32 | 2.30 | 5.26 |
| Cognitive empathy | 49.00 | 74.00 | 59.50 | 6.05 | 36.56 |
| Affective empathy | 28.00 | 46.00 | 36.21 | 3.75 | 14.05 |
| QCAE_Total | 77 | 114 | 95.71 | 8.15 | 66.34 |
| **AQ** | | | | | |
| Social skill | 1.00 | 7.00 | 2.47 | 1.64 | 2.68 |
| Communication | 0.00 | 4.00 | 1.53 | 1.33 | 1.77 |
| Imagination | 0.00 | 7.00 | 2.23 | 1.50 | 2.25 |
| Attention to detail | 1.00 | 9.00 | 5.15 | 2.28 | 5.22 |
| Attention switching | 0.00 | 8.00 | 3.65 | 1.94 | 3.75 |
| AQ_Total | 4 | 31 | 15.03 | 5.43 | 29.48 |
| **BVAQ** | | | | | |
| Emotionalizing | 10.00 | 35.00 | 17.82 | 6.40 | 40.94 |
| Fantasizing | 8.00 | 37.00 | 19.00 | 7.33 | 53.76 |
| Identifying | 8.00 | 35.00 | 19.15 | 6.45 | 41.64 |
| Analyzing | 8.00 | 35.00 | 16.35 | 6.67 | 44.54 |
| Verbalizing | 8.00 | 33.00 | 19.18 | 6.00 | 35.97 |
| BVAQ_Total | 52 | 150 | 91.50 | 25.40 | 644.56 |

*Note*. AQ = Autism-Spectrum Quotient; BVAQ = Bermond-Vorst Alexithymia Questionnaire; cEQ = cognitive subscale of the Empathy Quotient; IRI = Interpersonal Reactivity Index; QCAE = Questionnaire of the Cognitive and Affective Empathy. SD = Standard Deviation.

**Supplementary Table 2**

*Skewness, kurtosis and z-scores for each subscale and questionnaire for all subjects*

| Subscale | Skewness | | Z Skewness | Kurtosis | | Z Kurtosis |
|---|---|---|---|---|---|---|
| | Statistic | SE | | Statistic | SE | |
| **IRI** | | | | | | |
| Empathic concern | -1.17 | .403 | -2.90 | 2.12 | .788 | 2.69 |
| Personal distress | -0.18 | .403 | -0.45 | -0.54 | .788 | -0.68 |
| Perspective-taking | -1.25 | .403 | -3.10 | 2.46 | .788 | 3.12 |
| Fantasy | -1.13 | .403 | -2.80 | 1.13 | .788 | 1.42 |
| **EQ** | | | | | | |
| cEQ | 0.67 | .403 | 1.66 | -0.47 | .788 | -0.60 |
| **QCAE** | | | | | | |
| Perspective taking | 1.11 | .403 | 2.75 | 0.79 | .788 | 1.01 |
| Online simulation | -0.36 | .403 | -0.89 | 0.20 | .788 | 0.26 |
| Emotion contagion | 0.06 | .403 | 0.15 | 0.30 | .788 | 0.38 |
| Proximal responsivity | 0.37 | .403 | 0.91 | 0.03 | .788 | 0.04 |
| Peripheral responsivity | -0.97 | .403 | -2.41 | 0.82 | .788 | 1.05 |
| Cognitive empathy | 0.46 | .403 | 1.14 | 0.54 | .788 | 0.68 |
| Affective empathy | 0.15 | .403 | 0.38 | 1.08 | .788 | 1.36 |
| QCAE_Total | 0.21 | .403 | 0.51 | 0.07 | .788 | 0.08 |
| **AQ** | | | | | | |
| Social skill | 1.11 | .403 | 2.75 | 0.61 | .788 | 0.77 |
| Communication | 0.55 | .403 | 1.36 | -0.77 | .788 | -0.97 |
| Imagination | 0.83 | .403 | 2.06 | 1.50 | .788 | 1.90 |
| Attention to detail | -0.40 | .403 | -1.00 | -0.89 | .788 | -1.11 |
| Attention switching | 0.40 | .403 | 0.99 | -0.61 | .788 | -0.77 |
| AQ_Total | 0.80 | .403 | 1.98 | 1.24 | .788 | 1.57 |
| **BVAQ** | | | | | | |
| Emotionalizing | 1.10 | .403 | 2.73 | 0.69 | .788 | 0.87 |
| Fantasizing | 0.85 | .403 | 2.11 | 0.00 | .788 | 0.00 |
| Identifying | 0.36 | .403 | 0.89 | -0.36 | .788 | -0.45 |
| Analyzing | 1.40 | .403 | 3.47 | 1.51 | .788 | 1.92 |
| Verbalizing | 0.14 | .403 | 0.35 | -0.24 | .788 | -0.31 |
| BVAQ_Total | 0.81 | .403 | 2.01 | 0.31 | .788 | 0.39 |

*Note*. AQ = Autism-Spectrum Quotient; BVAQ = Bermond-Vorst Alexithymia Questionnaire; cEQ = cognitive subscale of the Empathy Quotient; IRI = Interpersonal Reactivity Index; QCAE = Questionnaire of the Cognitive and Affective Empathy. SE = Standard Error.

**Supplementary Table 3**

*Summary of terms associated with the activation of the seed region of interest from www.neurosynth.org*

| Associated term | Posterior probability | z-score |
|---|---|---|
| **rSMG (68, -38, 36)** | | |
| insula inferior | 0.91 | 5.55 |
| networks involved | 0.9 | 5.73 |
| attempt | 0.89 | 5.03 |
| fine | 0.88 | 4.71 |
| cortical motor | 0.88 | 4 |
| instructions | 0.87 | 4.3 |
| parietal lobules | 0.87 | 3.77 |
| supramarginal gyrus | 0.86 | 5.5 |
| ventral premotor | 0.86 | 4.85 |
| calculated | 0.86 | 4.48 |
| **rAG (52, -52, 22)** | | |
| beliefs | 0.92 | 10.53 |
| theory mind | 0.91 | 12.7 |
| mind ToM | 0.9 | 8.6 |
| ToM | 0.9 | 8.25 |
| temporoparietal junction | 0.87 | 8.76 |
| temporo parietal | 0.86 | 9.47 |
| parietal junction | 0.86 | 8.27 |
| mind | 0.85 | 9.56 |
| neocortical | 0.85 | 5.15 |
| junction | 0.84 | 9.81 |

*Note:* The first ten terms from www.neurosynth.org are ordered by their posterior probability, and in case of the equal value of the posterior probability by the z-score. Posterior probability indicates the probability of this term being used in the study, which reported activation in the given voxel. rAG = right angular gyrus; rSMG = right supramarginal gyrus; ToM = Theory of Mind.

**Supplementary Table 4**

*Summary of terms associated with the activation of the regions, whose resting state connectivity with the rSMG was linked to the individuals scores of empathy, alexithymia, or autism (www.neurosynth.org)*

| Associated term | Posterior probability | z-score |
|---|---|---|
| **Right insula (38, -4, 14)** | | |
| nociceptive | 0.89 | 6.53 |
| posterior insula | 0.88 | 7.67 |
| noxious | 0.88 | 6.46 |
| SII | 0.86 | 5.03 |
| sensation | 0.85 | 5.2 |
| **Thalamus (-4, -2, 8)** | | |
| incentive delay | 0.84 | 4.52 |
| anticipation | 0.77 | 4.93 |
| thalamus | 0.76 | 7.25 |
| caudate | 0.73 | 5 |
| nucleus | 0.71 | 4.41 |
| **rIOG (27, -100, 4)** | | |
| depended | 0.88 | 5.2 |
| inferior superior | 0.88 | 4.49 |
| videos | 0.86 | 3.99 |
| integrate | 0.85 | 4.66 |
| selectivity | 0.85 | 4.29 |
| **rMTG/rTP (51, 4, -26)** | | |
| mind ToM | 0.88 | 5.28 |
| ToM | 0.88 | 5.05 |
| anterior temporal | 0.87 | 6.92 |
| fronto temporal | 0.87 | 5.41 |
| indexed | 0.87 | 5.22 |
| **rMOrG (4, 62, -24)** | | |
| compulsive disorder | 0.97 | 7.24 |
| nineteen | 0.97 | 7.24 |
| SII | 0.97 | 7.12 |
| obsessive compulsive | 0.97 | 6.97 |

| | | |
|---|---|---|
| personality traits | 0.97 | 6.91 |
| **LiG (2, -90, -12)** | | |
| metabolism | 0.9 | 5.39 |
| vision | 0.87 | 4.71 |
| reward anticipation | 0.87 | 3.83 |
| vermis | 0.86 | 3.57 |
| younger | 0.85 | 4.67 |
| **lMOG/lOP (-10, -100, 11)** | | |
| mental imagery | 0.88 | 4.7 |
| watched | 0.88 | 4.53 |
| interactive | 0.88 | 4.49 |
| V1 | 0.86 | 4.03 |
| visual | 0.71 | 4.2 |
| **lMFG (-34, 60, 8)** | | |
| frontopolar | 0.87 | 5.37 |
| list | 0.85 | 4.41 |
| correspondence | 0.85 | 4.31 |
| memory tasks | 0.83 | 4.99 |
| mild cognitive | 0.82 | 4.32 |

*Note:* The first ten terms from www.neurosynth.org are ordered by their posterior probability, and in case of the equal value of the posterior probability by the z-score. Posterior probability indicates the probability of this term being used in the study, which reported activation in the given voxel. LiG = lingual gyrus; lMFG = left middle frontal gyrus; lMOG = left middle occipital gyrus; lOP = left occipital pole; rIOG = right inferior occipital gyrus; rMOrG = right medial orbital gyrus; rMTG = right middle temporal gyrus; rSMG = right supramarginal gyrus; rTP = right temporal pole; SII = secondary somatosensory cortex; ToM = Theory of Mind; V1= primary visual cortex.

**Supplementary Table 5**

*Summary of terms associated with the activation of the regions, whose resting state connectivity with the rAG was linked to the individuals scores of empathy, alexithymia, or autism (www.neurosynth.org)*

| Associated term | Posterior probability | z-score |
|---|---|---|
| **Left precuneus (-4, -56, 50)** | | |
| navigation | 0.89 | 6.45 |
| precuneus posterior | 0.87 | 5.81 |
| functionally connected | 0.86 | 4.54 |
| belief | 0.85 | 4.24 |
| imitation | 0.84 | 4.19 |
| **rOpIFG/rMFG (40, 16, 28)** | | |
| association cortex | 0.84 | 4.8 |
| distraction | 0.82 | 4.4 |
| aphasia | 0.81 | 3.94 |
| IFG | 0.74 | 4.51 |
| inferior frontal | 0.65 | 4.29 |
| **SMA (0, 14, 50)** | | |
| pre SMA | 0.77 | 7.52 |
| orthographic | 0.76 | 6.26 |
| motor pre | 0.75 | 4.88 |
| verbal working | 0.74 | 5.15 |
| SMA | 0.73 | 8.12 |
| **rPrG/IFG (52, 8, 16)** | | |
| mirror neuron | 0.79 | 4.51 |
| noxious | 0.79 | 4.2 |
| action observation | 0.78 | 4.38 |
| neuron | 0.77 | 4.24 |
| character | 0.77 | 4.17 |
| **lMTG (-45, -24, -13)** | | |
| balance | 0.91 | 6.24 |
| retrosplenial cortex | 0.9 | 5.13 |
| compensation | 0.88 | 4.68 |
| recall | 0.87 | 6.45 |

| | | |
|---|---|---|
| default network | 0.87 | 4.26 |
| **posterior lAG (-39, -60, 40)** | | |
| BA 40 | 0.83 | 4.19 |
| subcortical structures | 0.82 | 4.31 |
| memory retrieval | 0.79 | 5.5 |
| default network | 0.79 | 3.76 |
| judgments | 0.77 | 5.69 |
| **posterior rAG (39, -60, 58)** | | |
| preparatory | 0.89 | 6.61 |
| calculation | 0.86 | 3.99 |
| intraparietal sulcus | 0.75 | 4.27 |
| posterior parietal | 0.75 | 3.84 |
| intraparietal | 0.74 | 4.33 |
| **lMFG (-38, 29, 32)** | | |
| loop | 0.82 | 4.5 |
| DLPFC | 0.79 | 7.48 |
| cortex DLPFC | 0.79 | 6.66 |
| planning | 0.79 | 6.01 |
| preparation | 0.76 | 4.02 |
| **rMFG (32, 29, 28)** | | |
| major depression | 0.86 | 4.5 |
| engaging | 0.84 | 4.21 |
| remembered | 0.81 | 4.21 |
| autobiographical | 0.8 | 3.67 |
| DLPFC | 0.76 | 4.48 |

*Note:* The first ten terms from www.neurosynth.org are ordered by their posterior probability, and in case of the equal value of the posterior probability by the z-score. Posterior probability indicates the probability of this term being used in the study, which reported activation in the given voxel. BA 40 = Brodmann area 40; DLPFC = dorsolateral prefrontal cortex; IFG = inferior frontal gyrus; lAG = left angular gyrus; lMFG = left middle frontal gyrus; lMTG = left middle temporal gyrus; lSTS = left superior temporal sulcus; rAG = right angular gyrus; rMFG = right middle frontal gyrus; rOpIFG = right opercular part of inferior frontal gyrus; rPrG = right precentral gyrus; SMA = supplementary motor area.

**Abstract**

**English version**

The ability to differentiate between the mental states of oneself and those of others is crucial in social cognition. The right temporoparietal junction (rTPJ) was shown to be one of the core regions involved in self-other distinction. Furthermore, rTPJ was found to be comprised of subregions, which have distinct connectivity patterns and are associated with different processes. Moreover, evidence from the clinical research suggested that impairments in the Theory of Mind (ToM) and empathy in autism and alexithymia, can be related to the atypical functioning of the rTPJ. The first goal of this thesis was to investigate the functional connectivity of the two subregions within rTPJ, the right supramarginal gyrus (rSMG) and right angular gyrus (rAG), using resting state functional magnetic resonance imaging (rsfMRI). We further conducted an exploratory investigation of the trait-related modulations in the resting state networks. These empathy, autistic and alexithymic traits were assessed by the self-report questionnaires. Our sample consisted of 40 healthy female participants.

As expected the rSMG was functionally connected with brain regions, such as the bilateral insula, anterior- and midcingulate cortex, inferior frontal gyrus, which are involved in emotional processing, self-awareness and attention. The rAG showed connectivity with regions, such as the precuneus, temporal regions, medial prefrontal cortex, which are associated with mentalizing and the default mode network. The results of an exploratory analysis revealed modulations in the resting state networks related to the different aspects of empathy, as well as to the autistic and alexithymia traits. These findings can be useful for future clinical research and contribute to the better understanding of the rTPJ function.

**German version**

Die Fähigkeit, zwischen den mentalen Zuständen von sich selbst und Anderen zu unterscheiden, spielt eine bedeutende Rolle in der sozialen Kognition. Die rechte temporoparietale Übergangsregion (temporoparietal junction, rTPJ) ist eine der zentralen Gehirnregionen, die in diesem Prozess der Unterscheidung beteiligt ist. Die Forschung weist darauf hin, dass die rTPJ aus den Teilregionen besteht, die verschiedene funktionelle Konnektivität haben und mit unterschiedlichen Prozessen assoziiert werden können. Studien im klinischen Bereich zeigen auf, dass im Autismus und in der Alexithymie die Funktionsstörung der rTPJ und damit assoziierte Beeinträchtigungen in der Theory of Mind (ToM) und Empathiefähigkeit vorliegen. Das erste Ziel dieser Studie war die Untersuchung der funktionellen Konnektivität der Teilregionen von rTPJ, des rechten Gyrus supramarginales (rSMG) und des rechten Gyrus angularis (rAG), während Ruhebedingungen (resting state connectivity). Des weiteren wurde eine explorative Erforschung von an Persönlichkeitsmerkmalen (traits) gebundenen Modulationen in diesen Resting-State-Netzwerken durchgeführt. Diese Empathie, Autismus und Alexithymie Merkmale wurden mithilfe von Fragebögen erfasst. Die Stichprobe umfasste 40 gesunde weibliche Probandinnen.

Wie erwartet zeigte der rSMG die funktionelle Konnektivität mit Hirnregionen wie die bilaterale Insula, der anteriore und mittlere cinguläre Cortex und der Gyrus frontalis inferior, die mit der emotionalen Verarbeitung und Wahrnehmung, der Interozeption und den Aufmerksamkeitsprozessen assoziiert sind. Wir fanden eine hohe funktionelle Konnektivität zwischen den rAG und dem Precuneus, den temporalen Arealen und dem medialen präfrontalen Cortex - die Hirnregionen, die mit der Theory of Mind und den Default Mode Network in Verbindung gebracht werden. Zudem zeigten die Ergebnisse der explorativen Analyse die Modulationen in den Resting-State-Netzwerken, die mit den unterschiedlichen Aspekten der Empathie, des Autismus und der Alexithymie in Zusammenhang stehen. Die Ergebnisse dieser Studie können für die zukünftige Forschung im klinischen Bereich nützlich sein und zum besseren Verständnis der Funktion der rTPJ beitragen.