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Research Report

Emotional and cognitive aspects of empathy and their relation to social cognition—an fMRI-study

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ABSTRACT

The present functional magnetic resonance imaging (fMRI) study sought to characterize neural processes related to aspects of empathy and social cognition. It has been hypothesized previously that merely observing emotions in others automatically activates associated representations of the emotional state in the observer. We tested this prediction by presenting drawings depicting either one or two persons in an emotionally charged or neutral situation. Importantly and in contrast to previous imaging studies on empathy or social cognition, we did not instruct participants to assess the depicted persons' feelings or thoughts, but told them to simply watch the pictures to be able to perform a memory task unrelated to the main experimental question. This novel design allowed us to assess automatically elicited empathy-related effects (contrasting emotional and neutral situations) and to compare them with automatic social cognitive processes (contrasting stimuli with two persons vs. one person). We observed empathy-related increased hemodynamic responses in areas previously shown to be related to emotion processing (ventromedial and ventrolateral prefrontal cortex, PFC) and to social cognitive processes (superior temporal sulcus, STS, and medial PFC). The medial PFC activation was negatively correlated with participants' predisposition to feel distressed in emotional social situations, suggesting that interindividual differences in these higher-order functions might also impact empathic responses in social interactions.

1. Introduction

The *Encyclopedia Britannica* defines empathy as "the ability to imagine oneself in another's place and understand the other's feelings, desires, ideas, and actions." Even this short definition suggests that the concept of empathy is multifaceted. For example, Jean Decety and colleagues referred to the following as the main components of empathy: (i) an affective response to another person's feeling, which may or may not entail sharing the other's emotional state, (ii) the cognitive capacity to take the other's perspective, and (iii) regulatory mechanisms that keep track of the origins of the feelings (self vs. other) (Decety and Jackson, 2004). Empathy thus entails both affective components (sharing an emotional experience)

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and cognitive components (understanding the other's feelings).

An important theoretical advancement regarding empathy has been made by Preston and de Waal (2002) with their Perception-Action Model (PAM). Building on previous work on the "Perception-Action-Hypothesis," i.e. the idea that perception and action are represented in shared brain networks (Prinz, 1997; Rizzolatti and Arbib, 1998), the PAM states that the observation of another person's emotional state activates the observer's representations of that state, situation and person in an obligatory, automatic fashion. This representation in turn automatically generates associated autonomic and somatic responses, unless they are regulated or inhibited (Preston and de Waal, 2002). However, the hypothesis that emotions of others are obligatorily assessed by the observer (from the face, body or situational context) has not been adequately tested yet in the neuroimaging literature on empathy (for an overview of research about spontaneous assessment of others irrespective of empathy see Todorov et al., 2006).

Previous neuroimaging studies on empathy have mainly focused on shared representations between self and others with respect to basic emotions as pain or disgust (Jabbi et al., 2007; Jackson et al., 2005; Morrison et al., 2004; Phillips et al., 1997; Singer et al., 2004a,b, 2006; Wicker et al., 2003) or compared imagination of one's own or another's anger and fear (Preston et al., 2007). These studies show that seeing another person being disgusted or in pain elicits largely overlapping activations with feeling disgust or pain oneself (Jackson et al., 2005; Singer et al., 2004a,b). More specifically, both perceiving pain and observing a person in pain was related to activation in the anterior insula bilaterally (AI), the anterior cingulate cortex (ACC), the cerebellum and brainstem (Jackson et al., 2005; Singer et al., 2004a,b). However, these studies could not clarify to what extent brain regions underlying these processes are specific to empathy in contrast to other social cognitive processes. Moreover, the question to what extent these processes are elicited spontaneously, i.e. as a matter of course in the sense of the PAM has not been addressed.

Recently, some studies have thus aimed to compare directly thinking about people's feelings vs. people's beliefs or intentions (Hooker et al., 2008; Hynes et al., 2006; Shamay-Tsoory and Aharon-Peretz, 2007; Völlm et al., 2006), also dubbed "hot" and "cold" mental states (Amodio and Frith, 2006). One fMRI study, for instance, contrasted emotional and cognitive perspective-taking by showing the participants written stories and asking them questions regarding either the agent's feelings or cognitive state (Hynes et al., 2006). The authors reported common activations for both conditions in the medial prefrontal cortex (mPFC), the temporo-parietal junction (TPJ) and temporal poles and additionally found the left ventrolateral PFC preferentially activated for the emotional perspective-taking task (Hynes et al., 2006). In a similar vein but with non-verbal stimuli, Völlm and co-authors (2006) presented story cartoons asking participants to think either about the agents' intentions (Theory of Mind, TOM condition) or about their feelings (empathy condition). In contrast to the study of Hynes et al. (2006), the cognitive condition (TOM) led to higher activation in orbitofrontal regions (but right-lateralized), whereas the empathy condition yielded higher activation in the amygdala. In addition to these differential activations, overlapping activations were found in both conditions, including again the mPFC, the TPJ and temporal poles (Völlm et al., 2006).

Although this suggests that emotional and cognitive social processes have similar neural underpinnings, these overlapping activations might be caused by the task instructions alone. Importantly, in all these studies, participants were asked to think about the agent's mental state—either feelings or intentions. Such an instruction might artificially increase the similarity of involved neural processes. However, the PAM would predict that empathy-related emotional and cognitive processes are elicited *automatically* by the observation of others' emotional states (Preston and de Waal, 2002). This prediction cannot be tested with the above-mentioned operationalization of empathy. Given the suggested role of the mPFC in rather effortful social cognition such as mentalizing (Gallagher and Frith, 2003), the question arises, whether activity in this region is elicited by simply observing others' emotions.

The present study was aimed at further clarifying the neural substrate of perceiving and understanding others' emotions as a primary component of empathy (Decety and Jackson, 2004). To this end, we created a set of stimuli (Fig. 1) comprising situations in which either one person or two persons were shown in an emotionally neutral or emotionally negative situation. To avoid processes related to the registration of emotional facial expressions (Adolphs and Tranel, 2003; Adolphs et al., 1999; Sprengelmeyer et al., 1998), faces were deliberately left void of any features (eyes, nose, mouth).[1] Following Preston and de Waal (2002), we expected that the perception of a person's emotional state obligatorily (automatically) elicits an emotional response in the observer of the situation. Automatically, according to Preston and de Waal, means "as a matter of course, unless controlled or inhibited", "not requir[ing] conscious and effortful processing." We accordingly did not instruct the participants to consider the depicted person's feelings or thoughts, as it is usually done in empathy or mentalizing studies, but only asked them to watch the pictures carefully in order to be able to perform in a memory task, which was unrelated to the main experimental question. We were thereby able to investigate to what extent brain regions previously related to emotional and cognitive sub-processes of empathy would be activated without explicitly telling participants to focus on the observed person's feelings. Note that with the current approach we do not make the case for unconscious processing, but address the point of automatic in the sense of "as a matter of course."

First, we were interested in the contrast of emotionally charged and emotionally neutral situations to assess the effects of observing others' emotion and to test the predictions made by the PAM. More specifically, we reasoned that emotionally charged situations should lead to an empathic response in the observer whereas the neutral situations should not. Based on previous research on empathy, we expected

[1] The stimuli were inspired by similar style line drawings of the Adult Attachment Projective (AAP) that is used as a psychodiagnostic tool to assess attachment behaviour (George and West, 2001).

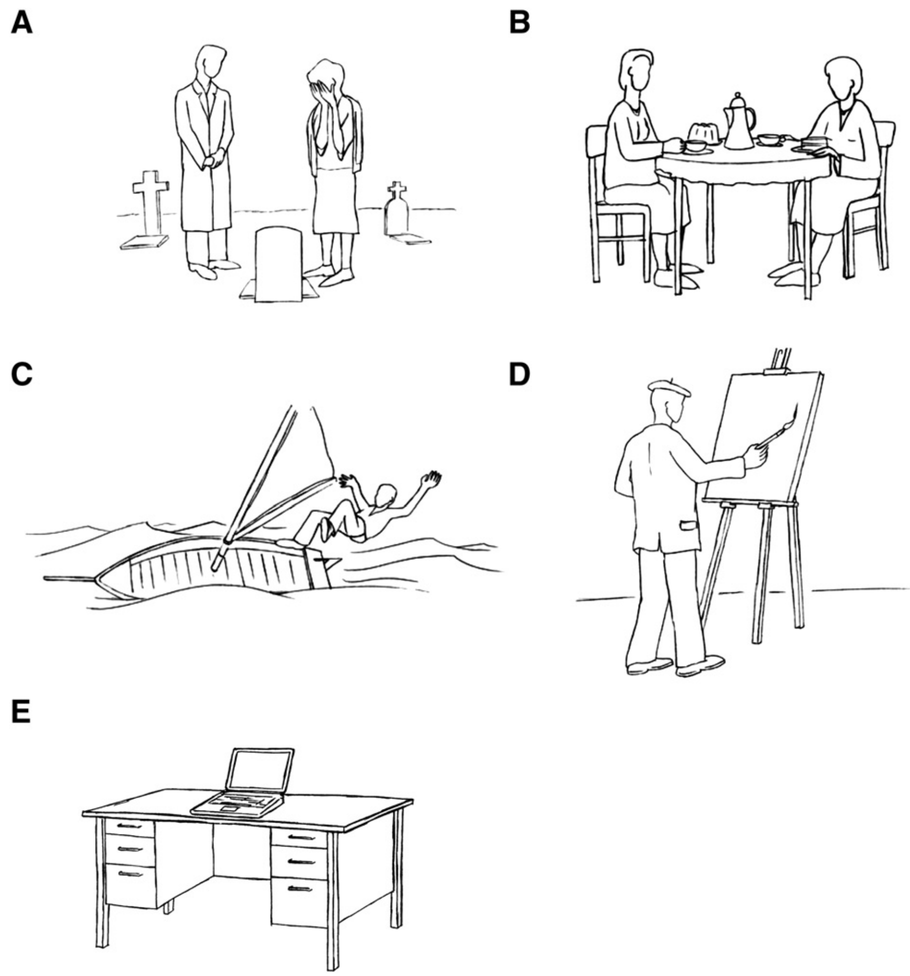

Fig. 1 – Example stimuli. Depicted are examples of the drawings from the five conditions: emotional content, two persons (A), non-emotional and two persons (B), emotional content, but only one person (C), non-emotional content, one person (D) and the control condition, in which only objects were depicted (E).

activations in orbitofrontal areas, amygdala, and insula, related to affective aspects of empathy, whereas cognitive aspects should be reflected in activations in the medial PFC.

Second, we were interested in comparing these results with social cognitive processes irrespective of any emotional content and thereby empathy. To this end, we contrasted the stimuli depicting a social relation (i.e. two persons) with those showing only one person. These stimuli differ in the amount of socially relevant information, but not in their emotional content. Moreover, several studies show that the observation of social interactions (Iacoboni et al., 2004) and thinking about social relations (Abraham et al., 2008; Kumaran and Maguire, 2005) activate areas typically seen for social cognitive tasks (i.e. mPFC, superior temporal sulcus, temporal poles, precuneus), suggesting that we process and understand social relationships through our ability to mentalize. Importantly, the study of Iacoboni and colleagues (2004) demonstrated activations in the mPFC, superior temporal sulcus (STS) and precuneus for the contrast of social vs. non-social video segments without instructing the participants to think about the agents' mental states. This suggests that observing interacting people obligatorily activates the suggested neural circuitry of social cognition (Adolphs, 2003). With the present design, we were able to directly compare automatic empathy-related processes on the one hand (emotional vs. neutral pictures) and cognitive processes directed to the understanding of social relations on the other hand (two vs. one person).

Finally, we wanted to investigate to what extent participants' disposition to empathize can predict activations in these regions. Previous studies demonstrate that a person's dispositional empathy was related to activity in the pain matrix when observing people suffering (Singer et al., 2004a,b). In a similar vein, we were interested in whether trait empathy correlates with participants' brain activations underlying their empathic response in the present task. Interindividual differences in the predisposition for empathy should affect neural activations in an experiment like the present, when participants are not explicitly instructed to empathize.

2. Results

2.1. Behavioral results and questionnaire data

Participants' test performance was close to perfect with on average 95% correct responses (range: 76.7–100%; s.d. = 6.2) showing that the participants indeed attended to the stimuli. With respect to the Interpersonal Reactivity Index (IRI; Davis, 1983a,b), participants' mean score on the Perspective Taking subscale was 16.9 (s.d. = 4.3), mean value on the Fantasy subscale was 13.9 (s.d. = 5.6), average score on the Empathic Concern subscale was 19.1 (s.d. = 4.0) and on the Personal Distress subscale 8.2 (s.d. = 4.4). There were significant sex differences in the Fantasy subscale ($t_{15} = -2.26$, $p = 0.039$) and the Empathic Concern subscale ($t_{15} = -3.37$, $p < 0.01$) with women scoring higher for both subscales.

2.2. *Imaging results*

2.2.1. *Emotional vs. neutral stimuli*

We first analyzed the main effect of emotional content by contrasting stimuli with emotional vs. neutral content (two or one person). Activations were observed in the dorsal part of the medial prefrontal cortex (mPFC), the ventromedial and left ventrolateral prefrontal cortex (vmPFC and vlPFC) and in the left superior temporal sulcus (STS). These areas showed a higher BOLD response for emotional compared to neutral content (Fig. 2 and Table 1). We also found activations in the right superior frontal gyrus, where an inverse pattern was detected, i.e. a decrease of activation related to emotional social stimuli and no change during presentation of neutral scenes. No activations were observed in the anterior insula or the amygdala, even when increasing the threshold to $p < 0.005$. However, with this threshold we detected activations in the right ventrolateral PFC and the right STS also, which argues against a strong lateralization of these effects.

Differences between the involved regions became apparent when taking a closer look at the time-course of activations (see BOLD time-course diagrams in Fig. 2). The BOLD response in both the mPFC and vmPFC showed an increased activation for emotional scenes compared to neutral scenes and scenes without any persons. In addition, the mPFC region suggested an effect of the social interaction with a higher BOLD response for two compared to one person (see analyses in the next paragraph). Moreover, emotional stimuli with two persons elicited the highest and most prolonged BOLD response in

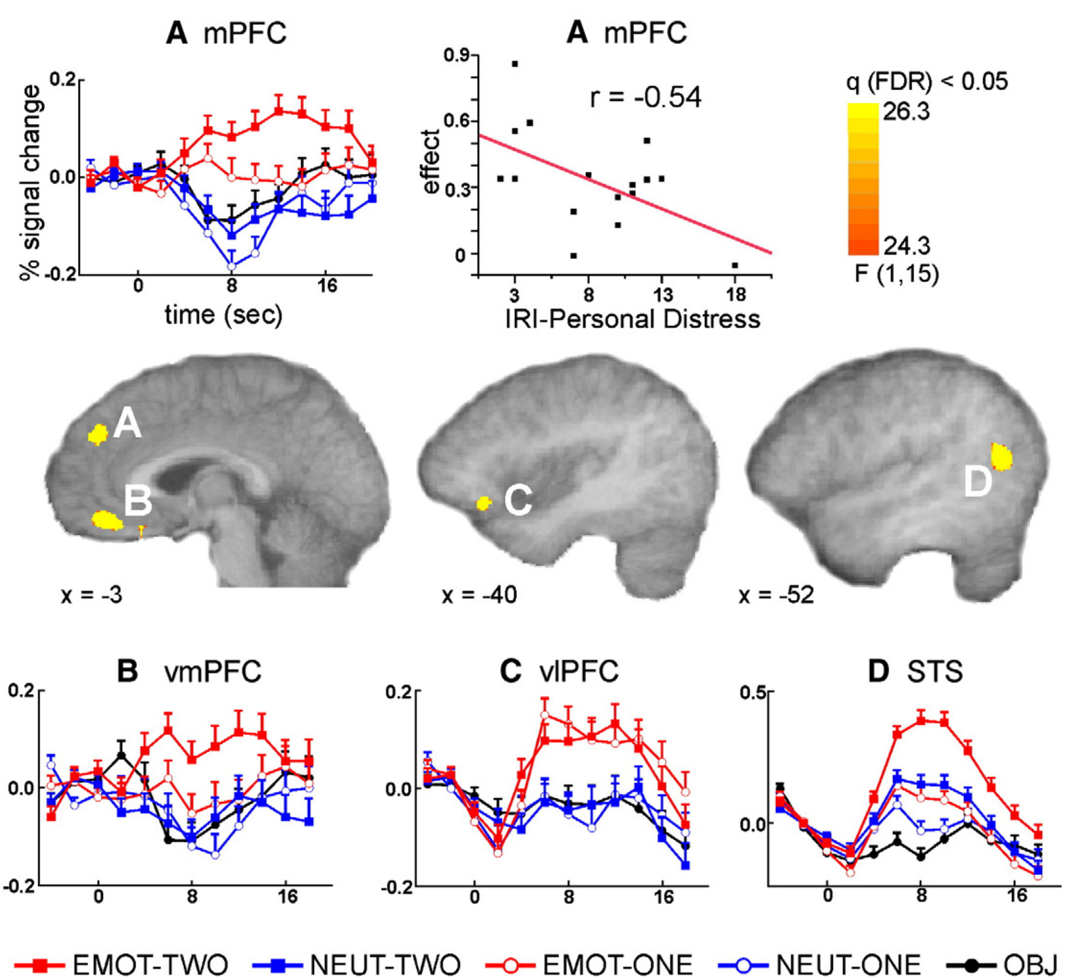

Fig. 2 – Emotional vs. neutral stimuli. Higher hemodynamic responses for emotional compared to neutral social stimuli and the corresponding event-related time-courses in the medial prefrontal cortex (A), the ventromedial (B) and ventrolateral prefrontal cortex (C). Note that "0" refers to the onset of the stimulus in every time-course. Also shown is the correlation of the emotion-related effect (difference in the beta values) in the mPFC with participants' scores in the IRI subscale Personal Distress (upper right diagram). Depicted is finally the emotion-related increased activity in the superior temporal sulcus (STS) and the corresponding time-course (D). A threshold of *q* (FDR) <0.05 was applied with a cluster threshold of 10 voxels.

Table 1 – Peaks of activation in Talairach coordinates.

Region of activation	Laterality	Coordinates	F-value (mean)
Emotional > neutral stimuli			
Superior frontal gyrus	R	31, 26, 51	26.8
Medial frontal gyrus	L	−2, 44, 34	27.8
Inferior parietal lobe	L	−63, −30, 28	30.5
Superior temporal sulcus	L	−49, −57, 13	27.7
Ventrolateral prefrontal cortex	L	−42, 28, −8	27.2
Ventromedial prefrontal cortex	L	−3, 38, −9	32.2
Neutral > emotional stimuli			
Superior frontal gyrus	R	39, 47, 25	28.7
Social relation > single person			
Precuneus	R	2, −55, 33	26.4
Cuneus	R	3, −80, 18	31.1
Superior temporal sulcus	L	−43, −65, 14	24.6
Middle temporal gyrus	R	55, −36, 7	19.3
	R	54, 3, −15	18.8
Superior temporal sulcus	R	47, −53, 13	25.1
Medial frontal gyrus	R	2, 44, 24	19.6
Middle frontal gyrus	R	50, 22, 22	16.8

both the mPFC and vmPFC suggesting that emotional content and social relation exerted an interactive effect on the activation in this area. However, this interaction did not yield significance (see ROI analyses below). The pattern in the vlPFC was different, revealing increased activity for emotional stimuli compared to the non-emotional stimuli, but no difference between stimuli with one or two persons was apparent (see statistics below). The STS demonstrated a higher increase for emotion-related stimuli in addition to an increase for two compared to one person and any compared to no person (see statistical analyses below).

2.2.2. *Social relation vs. single person*

Contrasting stimuli depicting a social relation vs. one person yielded activation in the different areas of the previously postulated neural circuitry of social cognition (Adolphs, 2003). Activations were observed in the medial PFC, several regions in the temporal lobe (right temporal pole, right middle temporal gyrus, superior temporal sulcus bilaterally), the precuneus, the dorsolateral prefrontal cortex (middle frontal gyrus) and in the occipital lobe (cuneus) (Fig. 3 and Table 1). The precuneus showed a reduced level of activation for the stimuli with only one person compared to social relation stimuli, but no difference between emotional or neutral stimuli. The right STS showed a similar pattern as the left STS, namely an increase for both emotion-related stimuli and stimuli with two compared to one person. In addition to the two main effects of the social relation and emotional content, an increased hemodynamic response to any compared to no person was obvious (see statistics below and BOLD time-course diagrams in Fig. 3).

2.2.3. *ROI analyses*

The activations observed for the main effects of emotion and the social relation were partly overlapping. More specifically, both conditions yielded activations in the left STS and in the mPFC. This suggests that processes involved in understanding others' emotions play a role also in analyzing social relations arguing against a content specificity. Note, however that the emotion-related mPFC activation was slightly more dorsal (~10 mm) compared to the social relation cluster. However, this could also be due to effects of the statistical threshold and might not reflect a real functional difference. We were thus interested in further specifying the degree to which the empathy-related effects can be explained by processes generally involved in social cognition.

We accordingly repeated the social relation contrast for the identified ROIs in the empathy-related contrast only. Note that this approach reduces the number of comparisons substantially, allowing us to apply a less restrictive statistical threshold (q (FDR) <0.05, $F_{1,15}$ >11.13, p (uncorrected) <0.005; cluster threshold of 10 voxels). We observed a significant social relation effect in the left STS only (Talairach coordinates: −48, −53, 13; average F-value: 21.6).

Although we had no specific hypotheses about interaction effects between the emotion and social relation factors, the event-related BOLD responses suggested possible higher emotion-related effects for social stimuli compared to single person stimuli (see Fig. 2). To analyze this, we tested for interaction effects between the two factors for the emotion-related ROIs only. However, no significant interactions were observed in these regions. This indicates that processes underlying empathy are not differentially involved as a function of social context.

2.2.4. *Person-related processes*

Finally, we performed an additional analysis to tap into the cognitive processes specific for person vs. object perception. To this end, we compared neutral scenes with one person to scenes with objects only (NEUT-ONE vs. OBJ). Areas activated for this contrast were found only in the posterior part of the temporal lobe, bilaterally. These areas were overlapping with the STS activation seen in the social interaction related and emotion related contrast (slightly more anterior and more ventral), which can be discerned in the respective BOLD time-courses in Figs. 2 and 3.

2.2.5. *Relationship with empathy questionnaire*

We observed a negative correlation between the emotion-related effect in the mPFC and participants' score on the Personal Distress subscale ($r = -0.54$, $p < 0.05$), such that people with no tendency to experience distress and anxiety in social situations showed the highest emotion-related effect in the mPFC (Fig. 2, upper right diagram). The social relationship effect in the mPFC showed a similar correlation with the Personal Distress subscale, which reached only marginal significance ($r = -0.44$, $p = 0.087$). No other correlations with subscales of the IRI were detected.

3. Discussion

The present study was aimed at investigating the neural basis of automatically elicited empathy-related effects and to compare them with automatic social cognitive processes. To this end, we presented pictures depicting either emotionally

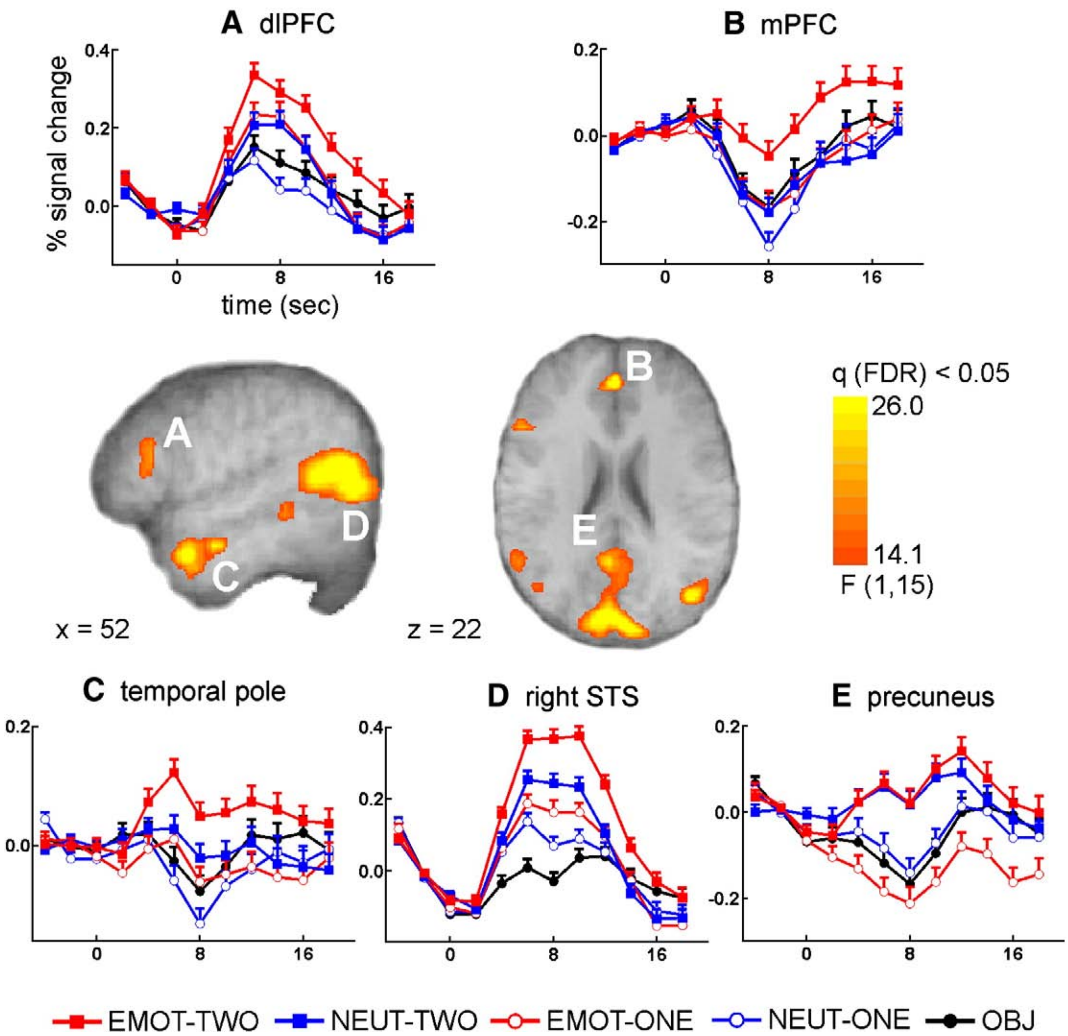

Fig. 3 – Social relation vs. single person. Higher hemodynamic responses for stimuli depicting social relations compared to one person only and the corresponding event-related time-courses in the right dorsolateral prefrontal cortex (A), the medial prefrontal cortex (B), the right temporal pole (C), the right superior temporal sulcus (D) and the precuneus (E). "0" refers to the onset of the stimulus in every time-course. A threshold of *q* (FDR) < 0.05 was applied with a cluster threshold of 10 voxels.

negative or neutral social scenes to induce empathic responses in the participants. By varying the number of depicted persons (two vs. one), we were able to compare the empathy-related processes with social cognitive processes aimed at analyzing the social relation. Importantly, we did not instruct participants to consider the depicted person's feelings or thoughts to tap into the emotional and cognitive sub-processes automatically elicited when watching persons in an emotional state and to thereby test predictions made by the PAM.

We observed higher activation for the emotional vs. neutral scenes in areas previously reported for person-related emotional processes (ventromedial and ventrolateral PFC) and in areas traditionally related to mentalizing or theory-of-mind related processes (STS and mPFC). Main effects for the social relation effect were observed in the previously postulated neural circuitry of social cognition (Adolphs, 2003), namely the mPFC, bilateral STS, the right temporal pole and the precuneus. Overlapping effects for the empathy and social cognition contrasts were observed in the left STS only. Although both contrasts elicited activations in the mPFC, the empathy-related cluster was slightly more dorsal. The data suggest that simply observing (a) person(s) in an emotional state activates regions previously related to both emotional and social cognitive processes, even without directing the observer's attention explicitly to the person's mental state. This extends previous neuroimaging studies as it demonstrates the degree to which empathy-related processes are elicited automatically (Preston and de Waal, 2002).

One caveat of the present study is that the memory task might have directed participants to focus on the emotions and social cues in the pictures to memorize the stimuli. As the social relations and emotions are quite salient features in the stimuli, participants might have used them to solve the primary task. As we did not ask participants about their strategy, we cannot fully exclude this alternative. However, as the memory task required participants to memorize the spatial configuration of the stimuli only (to judge whether the picture was presented as before or mirrored), it is unlikely that this explanation can fully account for the present results.

3.1. *Emotional aspects of empathy*

Previous neuroimaging research on emotional empathy has focused on the amygdala (Meyer-Lindenberg et al., 2008; Völlm et al., 2006), the anterior insula (Carr et al., 2003; Jabbi et al., 2007; Jackson et al., 2005; Singer et al., 2004a,b) and the orbital and ventrolateral frontal cortex (Blair, 2005; Hynes et al., 2006; Kawasaki et al., 2005; Shamay-Tsoory and Aharon-Peretz, 2007). In the present study, we observed increased activations in ventrolateral (inferior frontal gyrus) and ventromedial regions of the PFC for the emotional social stimuli compared to neutral social stimuli. The ventral part of the PFC has traditionally been implicated in the processing of reward and punishment related information, and more generally in the processing of emotionally relevant information, in particular within the context of decision-making (Kringelbach and Rolls, 2004; Rolls, 2000). Moreover, several studies have stressed its role in the regulation of social behavior, supposedly through its impact on the processing of affective social stimuli (Anderson et al., 1999; Bechara et al., 2000; Beer et al., 2006; Blair, 2004; Hornak et al., 2003). Only a few studies have implicated the ventral PFC in general theory of mind or mentalizing functions (Baron-Cohen et al., 1994; Völlm et al., 2006), stressing its role for processing affective stimuli—be they socially relevant or not (Rolls, 2000). This is further supported by lesion studies showing that patients with orbitofrontal lesions are impaired in processing socially relevant affective information (as in the faux-pas test), but not in mentalizing or theory of mind tasks (Blair and Cipolotti, 2000; Hornak et al., 2003; Shamay-Tsoory and Aharon-Peretz, 2007; Stone et al., 1998). These patients demonstrated deficits in the recognition of emotion expressions independent of cognitively demanding tasks or decision-making (Blair and Cipolotti, 2000; Hornak et al., 2003). Moreover, the lack of activation in the ventral PFC for the social relation contrast in the present study underscores the special role of the ventral PFC for the processing of *affective* information (Hynes et al., 2006). Note that as we presented a wide range of negative emotions and averaged across them, our paradigm does not allow us to make any more specific claims about the role of these areas in the emotional aspects of empathy. Further studies will be needed to assess possible differences in the (automatic) empathic response to various emotions.

In contrast to other studies on emotional empathy (Jackson et al., 2005; Singer et al., 2004a,b; Völlm et al., 2006), we did not observe activations in the amygdala or in the anterior insula. The amygdala has been implicated in a wide range of emotion-related processes including aversive and appetitive conditioning, instrumental learning and processing of emotional facial expressions or socially salient stimuli in general. (Adolphs and Tranel, 2003; de Gelder et al., 2004; Hooker et al., 2006; LeDoux, 2000; Morris et al., 1996; Phelps et al., 2000; Singer et al., 2004a,b). In our stimuli, no faces were depicted and emotions had to be inferred from the situational context and the persons' body posture. Such stimuli are less salient compared to emotional facial signals, which might explain the absent amygdala activation. The anterior insula has been implicated in the perception of pain and disgust (Jabbi et al., 2007; Jackson et al., 2005; Morrison et al., 2004; Singer et al., 2004a,b), i.e. emotions that were present only in very few (e.g., pain) or none of the current pictures (e.g., disgust). It might be that due to averaging across different emotions, those possibly emotion-specific activations did not yield significance. Further studies are needed to clarify whether empathy-related activations in the insula or amygdala are specific for observations of certain emotions as disgust or pain.

3.2. *Cognitive aspects of empathy*

In addition to the discussed activations in vmPFC and vlPFC, we observed an empathy-related increase of the BOLD response in the mPFC and the STS. The mediofrontal cortex has been implicated in a range of different social cognitive processes such as self-knowledge, person perception, mentalizing, interactions in cooperative or competitive games and false-belief tasks (Castelli et al., 2000; Fletcher et al., 1995; Gallagher et al., 2002; Gobbini et al., 2007; Gusnard et al., 2001; Mason et al., 2004; Mitchell et al., 2005; Schulte-Ruther et al., 2007). The mPFC has also been related to emotional processing (Lane et al., 1997; Phan et al., 2002), but this was observed in particular when participants had to reflect someone else's or one's own feeling, which again can be explained in terms of thinking about a mental state—that of another person or one's own. Gallagher and Frith (2003) have thus hypothesized that the function of the mPFC is specific to mentalizing and might lie in a "decoupling mechanism" that allows to process an agent's mental state which is "decoupled" from reality. This interpretation has been criticized by others, however (Ferstl and von Cramon, 2002; Zysset et al., 2002). Based on a direct comparison of tasks on pragmatic coherence and TOM, it has been argued that the mPFC is implementing rather domain-independent inference processes and, more generally speaking, the "initiation and maintenance of non-automatic cognitive processes" (Ferstl and von Cramon, 2002). Accordingly, mentalizing tasks are believed to be sufficient but not necessary to activate the mPFC.

Importantly, the mPFC activation in the current study was independent of any instruction or task-related need to focus on the agent's mental state or feelings. This shows that functions of the mPFC, be they specific to understanding others or more general for initiating volitional cognitive processes, are instantiated when observing persons in an emotional state and/or within a social relation even without any direct task-related demands. This extends previous studies on cognitive and emotional processes in empathy (Hynes et al., 2006; Völlm et al., 2006), as in these experiments participants were always instructed to consider other's mental states—either their feelings or their intentions. Interestingly, the maxima of activations for the two main effects were slightly apart from each other and did not overlap, as pointed out in the ROI analyses. This might indicate some distinction within the mPFC for rather social cognitive tasks and emotion-related processes. However, at least the similar correlations with the personality measure of empathy (see below) speak against a strong functional difference between the two activation clusters.

Interestingly, we found a negative correlation of participants' tendency for personal distress, as determined by the IRI (Davis, 1983a,b), and their emotion-related mPFC effect. This IRI scale assesses a person's tendency to perceive distress and anxiety when being confronted with an emotional social situation and might thus reflect a lack of regulatory abilities needed to keep track of the origins of one's emotion (Decety and Jackson, 2004). More specifically, personal distress arises, when people are not able to maintain a clear separation between self and other, which might be caused by a lack of mental flexibility and self-regulation, as has been proposed by Decety and Jackson (2004). It is intriguing to speculate on the basis of our results that the mPFC instigates or modulates such regulatory mechanisms. However, we did not observe any correlation with other IRI subscales, although previous studies have found them to be predictive of neural responses underlying empathy (Singer et al., 2004a,b). Clearly, replications of this finding and experiments tapping directly into the relationship of mPFC functions and the experience of personal distress are needed to substantiate this interpretation.

In addition to the emotion-related activations in prefrontal areas, we found an enhanced BOLD response for emotional compared to neutral stimuli in a posterior region of the temporal lobe (STS). In the same area, a clear differential activation for the social relation stimuli could be observed. Interestingly, this temporal region showed in addition to the emotion and social-relation effects an increase of activation when any compared to no person was depicted. This indicates that the STS activation does not reflect empathy-specific processes, but comes into play for a wide range of socially relevant stimuli including those eliciting an empathic response. In contrast to that the precuneus and temporal pole showed social-relation effects only, namely increased activity for pictures with two persons compared to those with one person. This replicates findings of Iacoboni et al. (2004), who reported higher activity in the STS and the precuneus, when people were passively watching videos of social interactions vs. video segments of one person only.

The STS has been reported consistently in all kind of mentalizing or theory-of-mind studies using different tasks such as story or cartoon understanding, biological motion perception, emotion recognition from body postures, perspective-taking, face perception and eye gaze processing (Calder et al., 2002; Castelli et al., 2000; Gallagher et al., 2000; Gobbini et al., 2007; Heberlein et al., 2004; Narumoto et al., 2001; Vogeley et al., 2001) as well as in a range of other tasks unrelated to social cognition, such as audiovisual integration or motion perception in general (Hein and Knight, 2008). It has been argued hence that the function of the STS is not specific to the attribution of mental states, but rather implements detection and understanding of other's goal-directed behavior and their intentions by integrating information from both the dorsal and the ventral visual stream (Allison et al., 2000; Gallagher and Frith, 2003). Moreover, it cannot be excluded that the STS activation, as well as the activations in occipital areas, are caused at least to some extent by a higher visual complexity of the stimuli with two vs. one person. Importantly however, this cannot explain the STS activation in the emotion contrast.

Some suggestions have been made about how STS activity might be further modulated by emotional or socially relevant stimuli (Allison et al., 2000). The STS is reciprocally connected to both the amygdala and orbitofrontal areas, i.e. brain areas that are highly relevant for the evaluation of socially salient and emotional stimuli as discussed before (Kringelbach and Rolls, 2004; Rolls, 2004). Feedback projections from these regions to the STS are accordingly assumed to amplify processing of salient social stimuli (Allison et al., 2000; Kringelbach and Rolls, 2004; Narumoto et al., 2001). In the present study, we did observe an emotion-induced increased BOLD response in the ventromedial PFC. It might be speculated that the evaluation of the social stimuli in prefrontal areas is driving the emotion-related differential response in the STS via feedback-projections and thereby strengthening the lower-level analysis taking place in the STS.

3.3. *Conclusions*

The present study aimed at identifying neural processes that are automatically elicited when observing others' emotions. We identified a network of prefrontal and temporal areas that has been associated earlier with affective aspects of empathy on the one hand and social cognitive processes as mentalizing and theory-of-mind on the other hand (Adolphs, 2001; Amodio and Frith, 2006; Gallagher and Frith, 2003). Moreover, based on the direct comparison with social cognitive processes independent of emotional aspects, we were able to dissociate differential roles of the involved prefrontal and temporal regions. These data provide evidence that observing others in an emotional state automatically initiates neural processes in medial prefrontal areas, that have traditionally been implicated in rather effortful, social cognitive tasks. The preliminary finding of an impact of participants' predisposition to empathize on mPFC activations suggests that interindividual differences in these higher-order cognitive processes might have an impact also on empathic responses and social behavior (Castelli et al., 2002).

4. Experimental procedures

4.1. *Participants*

Seventeen healthy volunteers (11 women; mean age = 27.8 years, s.d. = 4.8) took part in the experiment. All participants were right-handed (except one woman) and all were free of any psychiatric and neurological disorder (self-report). One woman was excluded from further analysis because of extensive movement during scanning; the results are accordingly based on the data of sixteen participants. Participants were paid and gave written informed consent. The study had been approved by the ethical committee of the University of Magdeburg.

4.2. *Paradigm*

The stimuli were black-and-white line drawings that had been custom-made for the present study. The drawings were assigned to five different conditions (examples are given in Fig. 1): Emotionally negative social situations involving two persons (EMOT-TWO), emotionally neutral social situations involving two persons (NEUT-TWO), emotionally negative situations involving one person (EMOT-ONE), emotionally neutral situations involving one person (NEUT-ONE), and scenes with objects only (OBJ). Negative depicted emotions included anger, sadness, pain or anxiety. Typical examples of the EMOT-TWO condition were “a man threatening a woman” or “two persons standing at a grave,” Typical stimuli of the NEUT-TWO condition were “two workers doing construction work” or “one person showing another one the direction”. Stimuli in the EMOT-ONE condition were, e.g., “a man falling from a sailing boat” or “a crying child,” Examples of the NEUT-ONE condition were “a man repairing a watch” or “an artist painting a picture,” The OBJ condition comprised drawings depicting for instance “a bike standing next to a house” or “a notebook lying on the desk” (not shown in Fig. 1).

Stimuli were rated for their emotional content in a separate study by a different sample of 29 students (15 women; mean age = 24.3). Participants were asked to rate their own negative emotional reactions to the pictures on a 7 point Likert scale (1 = “not at all” to 7 = “very strongly”). Additionally, they were asked to rate the depicted person’s negative emotions on a 7 point scale. This was asked for the stimuli showing one person only.[2] The stimuli of the EMOT conditions were rated higher on elicited negative emotions compared to the NEUT stimuli, both for stimuli involving one person (NEUT-ONE: mean rating: 1.4, range: 1.0–2.2; EMOT-ONE: mean rating: 5.0, range: 3.2–6.1) and two persons (NEUT-TWO: mean rating: 1.5, range: 1.0–2.3; EMOT-TWO: mean rating: 5.1, range: 2.6–6.9). Note that the range of ratings refers to the range across the stimuli not across the participants. The agent’s feelings on the EMOT-ONE stimuli were also rated more negative compared to the NEUT-ONE condition (EMOT-ONE: mean rating: 6.1, range: 3–6.9; NEUT-ONE: mean rating: 1.5, range: 1.1–2.9). We additionally analyzed how consistent these ratings were across subjects by averaging ratings within each picture condition (EMOT-TWO, -ONE, NEUT-TWO, -ONE) and testing for statistical significance by subjecting these values to paired-sample *t*-tests. All comparisons of interest (EMOT-TWO vs. NEUT-TWO and EMOT-ONE vs. NEUT-ONE) for both the participants’ emotion and the agent’s feelings were clearly significant (all $p < 0.0001$).

In each of three runs, drawings were presented in random order but with no more than two successive pictures of the same condition. Each picture was presented for 6 s, followed by a fixation cross (always 10 s), yielding a total trial duration of 16 s (slow event-related design). Each run comprised 40 pictures, 8 per condition. A picture appeared only once during the whole experiment. During scanning, participants were instructed to watch the pictures carefully. A short test phase followed each experimental run during which 10 of the previously presented pictures (two per condition) were shown. Half of the test pictures were presented in the same orientation as before, whereas the other half was shown mirrored. Participants had to indicate whether a picture was mirrored or not by button-press with the middle or index finger, respectively. No images were acquired during the test-phases and participants were informed about the test prior to the experiment.

[2] We asked six new participants (five women; age range 21-25) to rate the depicted persons’ emotions for the stimuli showing two persons also, separately for the two persons. We considered the highest value of a negative emotion as rating of the respective picture. Persons in the EMOT-TWO condition were rated higher in negative emotions (mean rating 6.4, range: 4.5 – 7) compared to persons in NEUT-TWO pictures (mean 1.8, range: 1 – 3.7). Ratings were very consistent across subjects, who significantly differentiated between the picture conditions ($t_5 = -24.3$, $p < 0.001$).

4.3. *Questionnaire*

The participants were asked to fill out a German version of the Interpersonal Reactivity Index (IRI; Davis, 1983a,b). This questionnaire comprises four 7-item subscales: Perspective Taking, Fantasy, Empathic Concern, and Personal Distress. The Perspective Taking subscale is related to social competence, higher self-esteem and interpersonal competence, but not to affective empathy. Scores on this subscale have been shown to predict their ability to match target persons with their self-descriptions (Bernstein and Davis, 1982). The Fantasy subscale taps the tendency to get deeply involved in the world of books, movies and plays and is correlated with verbal measures and intellectual abilities. The Empathic Concern subscale reflects a person’s tendency to have feelings of sympathy and concern for others. Scores on this subscale correlated with persons’ emotional reactions after exposure to a young woman in distress and the likelihood of subsequent helping behavior (Davis, 1983a,b). The Personal Distress subscale measures the tendency to experience distress and anxiety in overwhelming social situations such as emergencies.

4.4. *fMRI acquisition and analysis*

We used a 3-Tesla Siemens Magnetom Allegra Scanner to collect structural (T1-weighted MPRAGE: 256 × 256 matrix; FOV = 256 mm; 192 1-mm sagittal slices) and functional images (Gradient-Echo-EPI-sequence; TR = 2000 ms; TE = 30 ms; FOV = 192 mm; flip angle = 80°; matrix = 64 × 64; slice thickness = 3 mm; interslice gap = 0.75 mm; three runs of 325 volumes each). 32 transversal slices (3 × 3 × 3 mm voxel) parallel to the anterior commissure-posterior commissure (AC-PC) were obtained. Data analysis included preprocessing (slice scan time correction, 3D motion correction, temporal filtering), spatial smoothing (8 mm full-width at half-maximum Gaussian kernel), co-registration and normalization to Talairach stereotaxic space (Talairach and Tournoux, 1988) using Brain Voyager QX.

We performed random-effects analyses on the z-transformed functional data. We defined a GLM including the five different conditions as predictors, i.e. EMOT-TWO, EMOT-ONE, NEUT-TWO, NEUT-ONE, and OBJ. We performed an ANOVA with the factors emotional content (EMOT vs. NEUT) and social relation (TWO vs. ONE). In the first step, we were interested in the main effect of the emotional content to tap into empathy-related processes that are elicited by observing persons being sad, angry or afraid, and in the main effect of the social relation to tap into social cognitive processes unrelated to empathy. In a second step, we directly compared the two contrasts. Specifically, we created a mask from the activated regions in the emotion contrast and tested for social relation effects in these specific regions of interest (ROI analyses). As these two contrasts are assumed to be orthogonal, this analysis is not biased in the sense of ‘double-dipping’ (Kriegeskorte et al., 2009). We were thereby able to directly assess the degree to which the empathy-related effects were similar to cognitive processes unspecific for emotional content. In a third step, we contrasted the condition NEUTONE with OBJ to derive activations dissociating person- and object-perception related processes. Unless otherwise stated, statistical maps were created using a false discovery rate (FDR) of $q < 0.05$ with a cluster threshold of 10 voxels. The timecourses of significant regions of interest were created by averaging the signal change values of all voxels in the specific region relative to a 2-s prestimulus baseline for the time-window −2 to 18 s (where 0 is stimulus onset).

We finally extracted participants' average beta values from the regions-of-interest for the first contrast (EMOT vs. NEUT) to test for possible correlations (Pearson) with their IRI scores.

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