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Increased neural reactivity to socio-emotional stimuli links social exclusion and aggression

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ABSTRACT

We investigated changes in the neural processing of social information as possible link between social exclusion and aggression. Participants played a virtual ball game with two putative game partners, during which half of the 34 participants were excluded. Then, participants played the Taylor Aggression Paradigm (TAP) against the same partners. An empathy paradigm followed, in which participants watched pictures of neutral and emotional social scenes, while undergoing functional magnetic resonance imaging (fMRI). Excluded participants showed stronger neural reactivity to emotional compared to neutral pictures than included participants in regions associated with cognitive mentalizing and the mirror neuron system (bilateral superior, middle and inferior temporal gyrus, bilateral precuneus, right precentral gyrus). Reactivity of left inferior temporal gyrus and right precentral gyrus was positively correlated with aggressive behavior in the TAP. Our results support previous behavioral findings which suggest changes in social information processing as mediator between exclusion and aggression.

1. Introduction

1.1. Social exclusion and aggressive behavior

Forming and maintaining social bonds is considered a basic human need (Baumeister & Leary, 1995). Given the antisocial nature of aggressive behavior, it is somewhat counterintuitive that social exclusion, or interpersonal rejection, has been shown to elicit aggressive behavior in a variety of experimental settings (review in Leary, Twenge, & Quinlivan, 2006). Yet, ample evidence from longitudinal studies in children, for instance, indicates a vicious cycle of poor social skills or deficits in social information processing leading to peer rejection, which in turn increases antisocial behavior and negatively affects social information processing skills, making future peer rejection more likely (Lansford, Malone, Dodge, Pettit, & Bates, 2010; Miller-Johnson, Coie, Maumary-Gremaud, & Bierman, 2002). Evidencing such long-lasting effects, social exclusion during childhood was found to be associated with aggressive behavior in early adulthood (Rabiner, Coie, Miller-Johnson, Boykin, & Lochman, 2005).

Besides the long-term impact of social exclusion on aggression, numerous studies demonstrated short-term effects on antagonistic behavior. In an experimental setting involving both children and adults, Moor et al. (2012) found that in a dictator game (Cason & Mui, 1998) following exclusion in an online ball-tossing game, participants made more unfair offers toward those who excluded them than toward new partners. In a similar vein, Twenge, Baumeister, Tice, and Stucke (2001) found increased aggressive behavior in the Taylor Aggression Paradigm (TAP; Taylor, 1967) after participants were rejected by their peers. In contrast to the findings of Moor et al. (2012), aggression in this study was increased even toward new game partners, who had not been involved in the previous rejection.

1.2. Effects of social exclusion on social information processing

Different mechanisms have been suggested to mediate the relationship between social exclusion and aggression. According to the General Aggression Model of Anderson and Bushman (2002), frustration and subsequent negative affect, specifically anger, are common precursors of reactive aggressive behavior. However, in a meta-analysis of experimental and longitudinal studies on the consequences of rejection, Blackhart, Nelson, Knowles, and Baumeister (2009) come to the conclusion that “the immediate reaction to being rejected is a neutral emotional state rather than a negative one, on average.”

In a series of experiments by DeWall, Twenge, Gitter, and Baumeister (2009), participants who were told that they would likely be lonely in the future showed a cognitive bias toward aggressive words, which was associated with aggressive behavior toward their opponent in a reaction-time task. The authors conclude

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that increased aggression is a consequence of hostile cognition, rather than negative affect, leading the participant to perceive neutral information as antagonistic (DeWall, Twenge, et al., 2009). Increased attention to smiling faces and decreased attention to sad faces (DeWall, Maner, & Rouby, 2009), as well as reduced availability of emotional words (Twenge, Catanese, & Baumeister, 2003) after experienced or anticipated exclusion similarly suggest an effect of exclusion on the processing of socio-emotional stimuli.

Regarding the effect of exclusion on social information processing and its neural correlates, fMRI studies have highlighted changes in regions of the mentalizing network in particular. The mentalizing network comprises mPFC, TPJ, superior temporal sulcus (STS), temporal poles, inferior frontal gyrus (IFG) and precuneus and has reliably been found activated during the processing of socio-emotional stimuli (Carrington & Bailey, 2009; Singer, 2008). A subdivision into two partially overlapping neural networks reflecting cognitive theory-of-mind (ToM) processes (understanding the state of mind of another person) on the one hand and affective empathy (feeling the other person's emotions) on the other hand has been suggested. In his review, Lieberman (2007) concludes that cognitive ToM processes depend on a network including the dorsomedial PFC, STS, ventrolateral PFC and the lateral temporal cortex, whereas affective empathy is associated with a network including the anterior insula, the dorsal anterior cingulate cortex (dACC), ventromedial PFC (vmPFC) and medial PFC (mPFC), and also the dorsomedial PFC.

Cacioppo, Norris, Decety, Monteleone, and Nusbaum (2009) found that subjects scoring high on the UCLA Loneliness Scale (Russell, 1996) showed increased reactivity of occipital areas to negative social pictures, while non-lonely participants showed increased reactivity of the temporo-parietal junction (TPJ). The authors conclude that non-lonely participants are more likely to adopt the perspective of another person when seeing them in distress.

An effect of social exclusion on the processing of social stimuli was also observed by Powers, Wagner, Norris, and Heatherton (2011). In their study, participants were either told that they were likely to end up alone later in life, or to have many meaningful relations in their future (future alone paradigm; Twenge et al., 2001). Participants who had received the loneliness manipulation showed reduced activity in the medial PFC in response to negative social stimuli. The authors interpreted this as a protective mechanism, reflecting an avoidance of empathizing with or taking the perspective of people who pose a potential social threat.

These findings are in line with an experiment showing that excluded participants report less empathy with another person in distress (DeWall & Baumeister, 2006).

1.3. Current study

Combining the evidence from cognitive studies showing changes in social information processing after exclusion (DeWall, Maner, et al., 2009; DeWall, Twenge, et al., 2009; Lansford et al., 2010) and the above-mentioned neuroimaging results (Cacioppo et al., 2009; Powers et al., 2011), reactivity of the mentalizing network in response to socio-emotional stimuli seems a likely mediator of social exclusion effects on aggression. However, so far the effects of social exclusion on aggressive behavior and on neural reactivity to socio-emotional stimuli have not been investigated in a combined experimental design. In the following study, we combine the cyberball game described above, the Taylor Aggression Paradigm, and an fMRI-paradigm previously shown to reliably evoke activity in the mentalizing network (Krämer, Mohammadi, Donamayor, Samii, & Münte, 2010), such that changes in neural reactivity following exclusion can be related to aggressive behavior toward the perpetrators of the exclusion.

One well-established method for social exclusion in the laboratory is the cyberball game developed by Williams, Cheung, and Choi (2000), which has been adapted for the use with functional magnetic resonance imaging by Eisenberger, Lieberman, and Williams (2003). During cyberball, participants toss a ball back and forth in a virtual ball game with two ostensible partners. In the exclusion condition, the partners stop tossing the ball to the participant after a certain number of throws, thus excluding the participant from the game. In a recent fMRI-study using cyberball, Chester et al. (2013) found a positive correlation between the exclusion effect in the dACC and subsequent aggression in participants low in executive functioning, but the reverse effect in participants high in executive functions. However, this study did not address changes in social information processing after exclusion as possible mediator of the rejection–aggression relation.

The Taylor Aggression Paradigm (TAP) is a frequently used method for eliciting and measuring aggressive behavior in an experimental setting (Taylor, 1967). During the TAP, participants are led to believe that they are playing a competitive reaction time task against one or more opponents. Actually, both the opponent's behavior and the outcome of the reaction time task are under control of the experimenter. During each trial of the TAP, the winner of the task gets to punish the loser with an aversive stimulus of variable intensity. The intensity ostensibly chosen by the opponent serves as a manipulation of provocation, whereas the intensity selected by the participant serves as a measure of aggressive behavior. In its classical setting, the TAP simulates an opponent who selects increasing punishments during the course of the game, thus gradually increasing the level of provocation. Due to this provocative element, the TAP is considered a measure of reactive aggression. In their behavioral study investigating the effects of exclusion on aggression, Twenge et al. (2001) used as aggression measure only the first trial of the TAP. At this point, participants had not received any punishment from their opponent. Thus, this measure reflects the provocative effect of the exclusion experience independent of provocation during the TAP. In the current study, we were also interested in the effect of the exclusion alone and modified the TAP, such that the participant received only low to medium levels of punishment. In this form, the participants' aggressive behavior in the TAP is unprovoked.

On a behavioral level, we expected that participants who were excluded during the cyberball game would select higher punishment levels during the TAP, thus acting more aggressively toward their putative game partners. On a neural level, we expected that regions of the mentalizing network would show differential reactivity to socio-emotional stimuli for included vs. excluded participants, mediating the effect of social exclusion on aggressive behavior.

2. Methods

2.1. Participants

40 healthy volunteers (17 male) participated in this study. Participants were free of neurological and psychiatric disorders and all but two were right-handed (self-report). Mean age of the participants was 22.5 years (range 19–28). All participants gave written informed consent and received 7 Euro per hour as compensation for their participation. The study was approved by the local ethics committee and performed according to the Declaration of Helsinki.

2.2. Procedure

Upon arrival in the laboratory, participants were introduced to two game partners for the experiment, one male and one female,

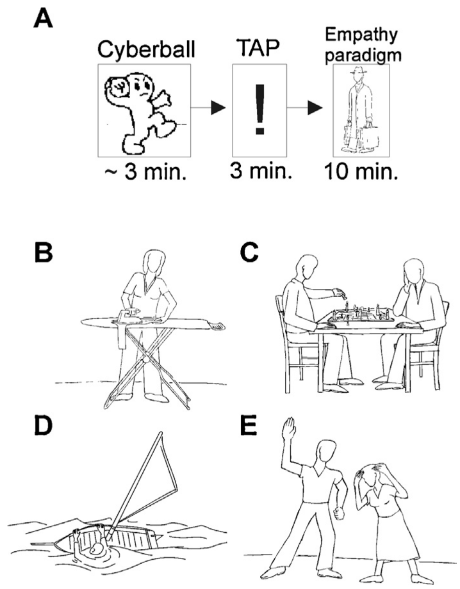

Fig. 1. Experimental paradigm. A shows the time course for the experiment. Example pictures for the four categories of the empathy paradigm are given: neutral single (B), neutral social (C), emotional single (D) and emotional social (E).

who were confederates of the experimenter. Together with the confederates, participants received written instructions. Then, participants entered the MRI-scanner. The experiment began with a game of cyberball. Participants were randomly assigned to one of two conditions (exclusion or inclusion). After the cyberball game, participants engaged in the TAP, ostensibly playing with the same partners as during cyberball. Finally, the empathy paradigm was performed. Even though we assumed, based on theoretical assumptions, that neural aftereffects of exclusion should precede behavioral effects, we chose this order of paradigms to avoid behavioral priming by the pictures of the empathy paradigm, as some pictures of the negative-social category depict aggressive scenes. For the cyberball and TAP games, participants and their opponents were represented by cartoon characters, so participants did not know during the TAP, which opponent they were playing against. For practical reasons and to prevent the need for interaction with the participant during the experiment, all three tasks were performed inside the MRI-scanner, although only the empathy paradigm was designed as an fMRI-task. We used the cyberball paradigm only as experimental manipulation and not as dependent measure and therefore did not analyze BOLD changes during the game itself. For the TAP, the timing of the stimuli would have precluded an analysis of BOLD changes, as our aim was to keep the duration of the game as short as possible. The time course of the experiment is given in Fig. 1A.

Following the MRI-measurements, participants filled out a post-experimental questionnaire testing for suspicions about the true aims of the study, as well as personality questionnaires. Finally, participants were fully debriefed, paid and thanked for their participation.

2.3. Cyberball

For the cyberball game, participants were instructed that they would be tossing a ball back and forth in a virtual ball game with the two other participants. The game consisted of 60 throws in total. During the first half of the game, participants received the ball in one third of trials. During the second half, participants either received the same ratio of throws (inclusion condition), or did not receive any more throws (exclusion condition). We chose to include all participants during the first half of the game in order to ensure that participants believed the program was working and that their co-players had correctly understood the instructions.

2.4. Taylor Aggression Paradigm

After the cyberball game, participants played 14 trials of the TAP, 7 trials against each opponent. Each trial consisted of three phases: at first, the participant was informed against which opponent (represented by the respective cartoon character) he or she was playing and selected a punishment level for the opponent, in case the participant wins. Punishment was implemented as an aversive noise which could be adjusted in terms of loudness on a scale from 1 to 8. After punishment selection, participants engaged in the reaction time task, pressing a button as quickly as possible in response to a visual stimulus. Finally, the participant was informed whether he or she had won or lost and which punishment level the opponent had selected. In case of losing, the punishment noise was presented in the respective noise level via headphones. Participants won 50% of trials. The order of the trials participants played against the two opponents, as well as winning and losing, was randomized. Both opponents selected low to medium levels of punishment (range 1–5, mean = 2.6). To increase the credibility of the experiment, we included seven additional trials, during which participants saw the word “pause” on the screen. They were told that during these pauses, their two opponents would be playing against each other.

2.5. Empathy paradigm

For the measurement of neural reactivity to socio-emotional stimuli, participants were presented with black-and-white drawings of four categories: neutral single (one person performing a neutral action, such as ironing), neutral social (two people interacting in a neutral manner, such as playing chess), emotional single (one person in distress, such as falling off a boat) and emotional social (two people interacting in an aversive manner, such as a man hitting a woman). Examples of each category are given in Fig. 1B–D. Pictures were presented in 8 blocks, with 2 blocks per category. Each block contained 8 pictures of one category. Pictures were presented for 4 s with 2 s of blank white screen in between. Between blocks, a black crosshair on a white background was presented for 30 s. The order of the blocks was the same for all subjects. The order of the stimuli within each category was randomized.

In order to ensure participants were paying attention to the stimuli, they were instructed to perform a memory-task during picture presentation. Participants were told that following the presentation, some of the pictures would be presented again, either mirrored or in the original orientation. At the end, eight pictures (two of each category, four mirrored) were presented again and participants had to indicate by button press, whether a given picture was mirrored or not.

This paradigm has previously been shown to increase activity in the mentalizing network, which was related to the personal distress subscale of the interpersonal reactivity index (Davis, 1983; Krämer et al., 2010).

2.6. MRI measurement

For MRI measurements, we used a 3-T Philips Achieva scanner. During the empathy paradigm, we obtained 303 volumes of functional images with the following specifications: Gradient-Echo-EPI-Sequence; TR = 2000 ms; TE = 30 ms; FOV = 192 mm; flip angle = 80; matrix = 64×63; slice thickness = 3.0 mm; gap = 0.3 mm; 34 transversal slices; in-plane voxel size = 3.0×3.0 mm. During the cyberball game and during the

TAP, functional images with the same specifications (but only 100 and 95 volumes) were obtained to ensure consistency with the cover story, but were not analyzed. After the empathy paradigm, we obtained structural images (T1-weighted; FOV = 240 mm; matrix = 240 × 240; 180 sagittal slices of 1 mm thickness).

2.7. Personality questionnaires

After the measurements, participants filled out the German version of the Buss and Perry Aggression Questionnaire (AQ; Herzberg, 2003) and the Interpersonal Reactivity Index (IRI; Davis, 1983) in our own translation.

The AQ contains three subscales: physical aggression, verbal aggression and hostility. The IRI consists of four subscales: perspective taking (PT), a fantasy scale (FS), empathic concern (EC) and personal distress (PD).

2.8. Data analysis

Participants were excluded from the analysis if they showed head movements exceeding 4 mm during the empathy fMRI paradigm (nobody) or if they guessed the true purpose of the experiment (five participants). One participant was excluded because he showed head movement of 3 mm during the functional run and also moved during the T1-weighted scan causing the co-registration to fail. Thus, 34 participants (14 male) were included in the final sample. Of these, 16 were in the experimental group (exclusion), 18 in the control group (inclusion).

2.9. Behavioral data

For the TAP, each participant's punishment selections were averaged over all trials into one mean selection score which was used as a measure of aggression against the opponents. Since participants did not know which opponent was represented by which cartoon character, and opponents did not differ in their behavior, we did not analyze punishment selections for the opponents separately.

To assess the rate of unprovoked aggression in the experimental groups, we counted the number of high punishment selections made by each participant. Since the highest selection made by the opponents was 5, selections of 6 or higher were considered unprovoked aggression. We then performed the Mann–Whitney-*U* test to compare differences in total number of high selections between the groups.

To investigate the relationship between aggression and personality factors, we correlated data from the AQ and IRI questionnaires with the mean punishment level selection during the TAP.

2.10. fMRI data

For all MRI-analyses, we used SPM8, an open-source, Matlab-based toolbox (Wellcome Trust Centre for Neuroimaging, London). Functional images were preprocessed using standard procedures: temporal adjustment for differences in slice time acquisition, motion correction, co-registration of EPI images with T1-weighted structural images, segmentation of structural images, normalization into MNI-space and spatial smoothing with an 8 mm kernel. In order to improve the co-registration step, T1-weighted images were first co-registered to a gradient echo EPI. We then used both images for co-registration with the mean functional image.

For two participants, 2–3 consecutive trials of the empathy paradigm were excluded from the analysis, because they showed rapid head movement during these trials, which interfered with the model fit but did not meet the 4 mm cutoff criteria.

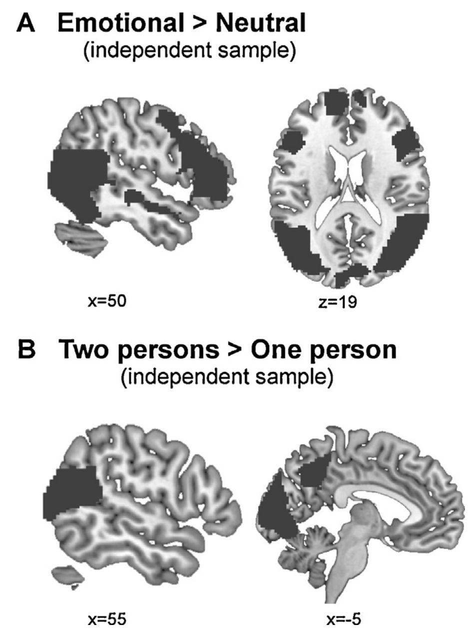

Fig. 2. Functional brain mask. Masking images derived from an independent sample of 27 participants using the same stimuli as the current study are shown for the emotional > neutral contrast (A) and the social > single contrast (B).

Functional images for the empathy paradigm were analyzed using a general linear model (GLM). On a single subject level, a design matrix including the four conditions set up as a block design, as well as the motion regressors from the motion correction step in the preprocessing, was set up. Four contrasts were defined on this level: neutral (weighting neutral blocks containing both social and single pictures of neutral valence positively), emotional, single (containing non-social pictures of both neutral and negative valence) and social, each against baseline. Since threefold interactions cannot be modeled in SPM and we did not have hypotheses concerning threefold interactions between the factors group (exclusion vs. inclusion), emotion (emotional vs. neutral pictures) and social (social vs. single pictures), we set up two 2 × 2 factorial GLMs on the second level, modeling the factors emotion and social separately. Both models included the factor experimental group, the respective within-subject factor and an interaction factor.

For analysis of the functional data, we created masks using functional data from another, independent sample comprising 27 participants. These data were obtained from a study using the same stimuli used in this study (plus pictures of an additional condition showing objects, which was not included in the current study), in an event-related design (experimental design was exactly like in Krämer et al., 2010). Using activation maps for the contrast emotional vs. neutral, we created a functional brain mask using a significance threshold of $p < .05$ false-discovery-rate (FDR) – corrected (Fig. 2A). This mask was used for the group level model with the factor emotion, such that only voxels which showed increased activation for this contrast in the independent sample were included in the analysis. The same procedure was followed for the contrast social vs. non-social (Fig. 2B). This approach lowered the number of statistical tests and limited the analysis to brain regions for which we had a priori hypotheses about their involvement in mentalizing processes.

Brain regions that showed an interaction between social exclusion (between-subject factor) and picture content were defined as functional regions of interest (ROIs). In order to investigate whether exclusion effects on neural responses to socio-emotional stimuli were related to aggressive behavior, we regressed mean aggression scores against the averaged individual contrast values for these ROIs using the SPM-toolbox marsbar (Brett, Anton, Valabregue, & Poline, 2002), such that the number of statistical tests performed equaled the number of ROIs. For those regions that showed a significant relationship between neural reactivity and aggressive behavior, we tested whether this relationship constituted a mediational effect. For this analysis, we used the bootstrapping approach described by Preacher and Hayes (2008) as implemented in their mediate-SPSS-macro. We generated 5000 samples, using experimental condition as independent variable (X), mean punishment selection as dependent variable (Y) and mean contrast value of the respective ROIs as mediators. In this analytical approach, the bias-corrected 95% confidence interval for the inference about an indirect effect of X on Y is estimated. If this confidence interval does not contain zero, the indirect effect can be interpreted as nonzero.

For all GLM analyses, we used a significance threshold of $p < .05$ FDR-corrected with a minimum cluster size of 20 voxels. For the regression of ROI-data against aggression scores, we used a significance threshold of $p < .05$ uncorrected.

3. Results

3.1. Postexperimental questionnaire

Participants in the exclusion group rated their opponents' behavior for the whole experiment as less fair than participants in the inclusion group (means −.47 and .92; SE = .37; $t_{32} = 3.78$; $p = .001$; Cohen's d (mean difference/pooled standard deviation) = 1.10) and all participants in the exclusion group reported that they noticed the exclusion. However, nine of the 16 participants in the exclusion group reported that they believed their opponents had been instructed to exclude them during the second half of the cyberball game. Since these participants did not express any suspicion about the nature of the TAP, and previous studies found strong negative effects of ostracism during cyberball even when participants were told that they were playing against a computer (Onoda et al., 2010; Zadro, Williams, & Richardson, 2004), we did not exclude these participants from the analysis but used suspicion as a possible confound in the analyses.

3.2. Behavioral effects

Participants in the exclusion and inclusion groups did not differ significantly in their mean punishment level (mean exclusion = 3.1; mean inclusion = 2.6; $t_{32} = 1.27$; $p = .21$; $d = 0.45$).

When splitting the group further considering whether excluded participants became suspicious or not (experimental group – suspicious; experimental group – non-suspicious; control group), we found a significant group effect (univariate ANOVA with factor group: $F_{2,33} = 8.56$; $p = .001$). Post hoc t-tests showed that participants in the non-suspicious group selected significantly higher punishments (mean = 4.08; SE = 0.31) than participants in the suspicious group (mean = 2.28; SE = .23; $t_{14} = 4.76$; $p = .001$; $d = 1.54$) and in the control group (mean = 2.58; SE = .25; $t_{23} = 3.38$; $p = .003$; $d = 1.43$), whereas there was no difference in punishment level selection between the suspicious participants and those in the control group ($t_{25} = -.77$; $p = .45$; $d = 0.32$; Fig. 3A). However, these results should be treated carefully, as the sample size for the suspicious and non-suspicious groups was small ($n = 9$ and 7, respectively).

The comparison of rate of unprovoked aggression (numbers of high selections) between excluded and included participants did not reach significance ($Z = -1.6$; $p = .055$ one-sided). The comparison between controls, non-suspicious and suspicious excluded participants using the Kruskal–Wallis test showed a significant difference between groups ($\chi^2 = 12.45$; df = 2; $p = .002$). Non-suspicious participants made significantly more high selections than suspicious excluded participants ($U = 6.0$; $U_{\text{crit } 7,9} = 9$ for $p < .01$ one-sided; Fig. 3B). We also found a significant difference for the comparison between non-suspicious and control subjects ($U = 16.5$; $U_{\text{crit } 7,18} = 24$), whereas there was no difference between suspicious and control subjects ($U = 75$; $U_{\text{crit } 9,18} = 36$).

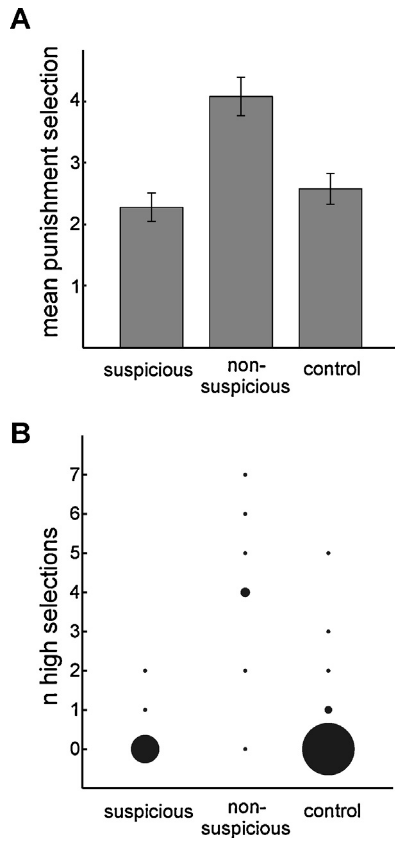

Fig. 3. Aggressive behavior in the TAP. A shows the mean punishment selections for excluded participants who were suspicious, believing their opponents had been instructed to exclude them, excluded non-suspicious participants and the control group. In B, distribution of participants over absolute number of high (>5) selections is given for the same three groups. The number of participants represented by one data point is indicated by the size of the data point (range 1–13).

Finally, we found a positive correlation between the hostility subscale of the AQ and aggressive behavior ($n = 34$; $r = .49$, $p < .01$). Importantly, the two experimental groups did not differ for hostility scores ($p > .6$). A negative correlation between aggressive behavior and the perspective taking subscale of the IRI approached significance ($n = 34$; $r = -.34$; $p = .052$). There was no significant correlation between any of the other personality measures and aggression ($n = 34$; r between −.03 and .126; p between .241 and .867).

3.3. Neural reactivity to socio-emotional stimuli

The main effect of emotion (contrasting emotional vs. neutral pictures over all subjects) showed increased activity in the bilateral inferior frontal gyrus (IFG), in the mPFC, the bilateral superior temporal gyrus (STG), the left inferior parietal lobule (IPL) and the right supplementary motor area (SMA) (Fig. 4A and Table 1). The main effect of social (contrasting social vs. single pictures over all subjects) showed increased activity in the bilateral cuneus/precuneus and in the MTG extending to the STG (Fig. 4B and Table 1).

There was no significant main effect for the factor group (included vs. excluded, across both the suspicious and non-suspicious participants).

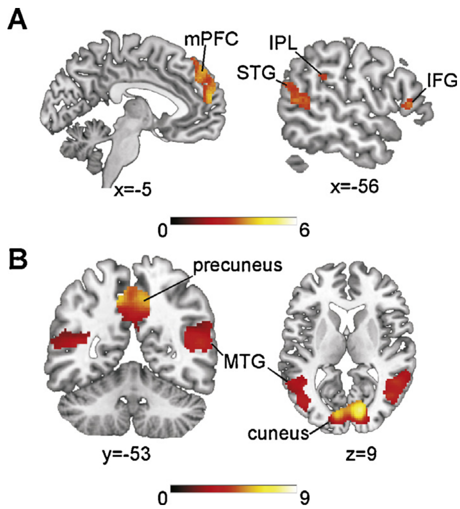

Fig. 4. Main effects for the empathy paradigm. Neural activation patterns are shown for the emotional > neutral contrast (A) and the social > single contrast (B) at a significance threshold of $p < .05$ FDR-corrected, cluster threshold = 20 voxels.

Table 1
Neural activations for the empathy paradigm.

Region	Hemisphere	X, Y, Z	t-Value
Main effect emotional > neutral			
Inferior frontal gyrus	R	52, 20, 0	5.01
	L	−50, 24, 8	4.14
Superior temporal gyrus	L	−60, −58, 16	3.97
	R	54, −52, 8	3.14
Medial frontal gyrus	L	−8, 58, 20	4.37
Inferior parietal lobule	L	−62, −32, 26	3.5
Superior frontal/precentral gyrus	R	8, 8, 64	3.68
Interaction experimental group × emotion			
Inferior temporal gyrus	L	−44, −54, −10	3.79
	R	48, −48, −12	3.5
Superior temporal gyrus/insula	L	−42, −52, 8	4.4
	R	44, −40, 18	3.86
Middle temporal gyrus	L	−38, −76, 20	4.73
	R	44, −72, 18	4.65
Cuneus/precuneus	L	−24, −80, 32	3.71
	R	20, −70, 38	3.57
Precentral gyrus	R	44, −4, 44	5.44
Main effect social > single			
Cuneus	R	12, −80, 4	9.41
Middle temporal gyrus	R	42, −64, 8	4.65
	L	−40, −70, 16	4.55

The interaction analysis showed a significant interaction between experimental group and emotional content for the right precentral/middle frontal gyrus, the bilateral precuneus, the bilateral MTG, the right posterior insula/STG, the left STG, the inferior temporal gyrus bilaterally, extending to the fusiform gyrus on the left hemisphere (Fig. 5A and Table 1). Post hoc between-group *t*-tests showed that these areas were more strongly activated for the emotional vs. neutral contrast in the exclusion group than in the inclusion group (Fig. 5C). As Powers et al. (2011) reported a modulating effect of social exclusion on mPFC activity, we specifically examined the mPFC cluster that we found activated

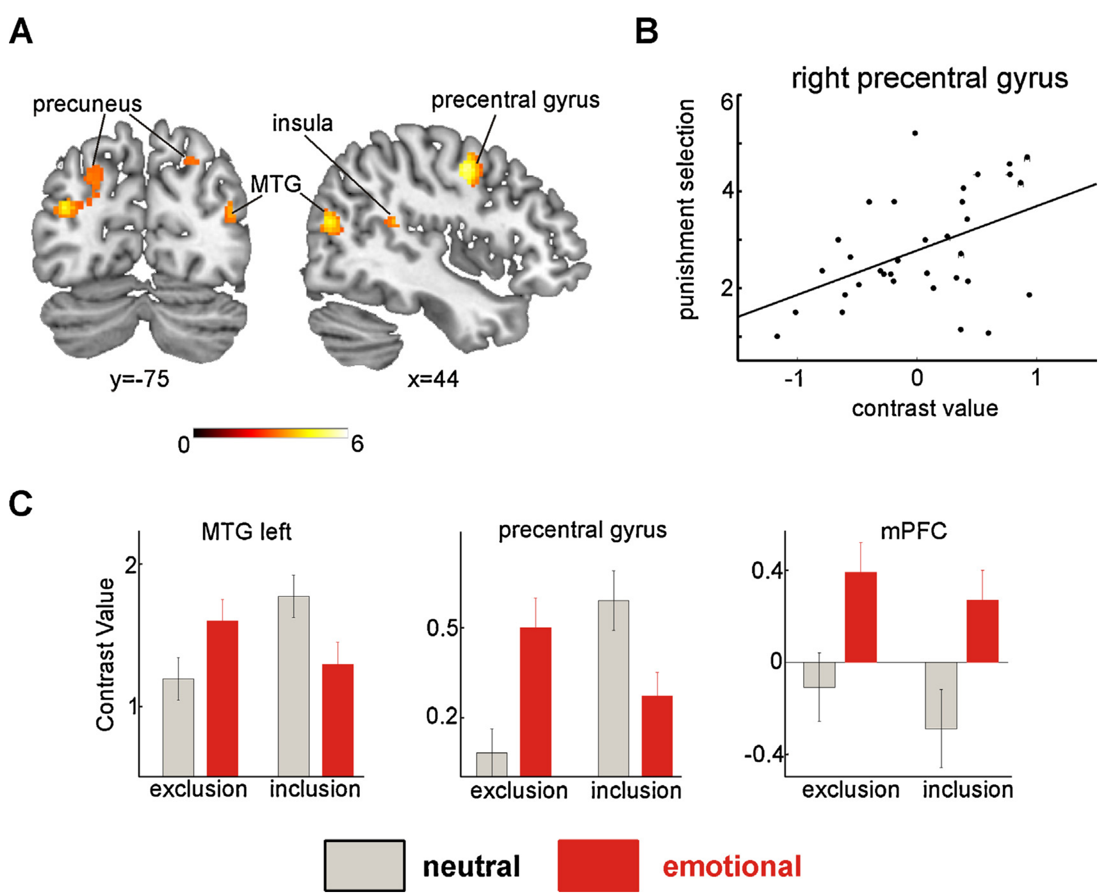

Fig. 5. Interaction effects between exclusion and emotional valence. Neural activation patterns for the interaction experimental group × emotion in the empathy paradigm are shown in A at a significance threshold of $p < .05$ FDR-corrected, cluster threshold = 20 voxels. The correlation between the emotional > neutral contrast value for the precentral gyrus ROI and the mean punishment level selection is shown in B. Mean contrast values for emotional and neutral pictures are shown separately for excluded and included participants (C) for the left middle temporal gyrus (MTG), the right precentral gyrus and the medial prefrontal cortex (mPFC) regions of interest (ROI).

for the main factor emotion > neutral. Fig. 5C depicts the mean contrast values for emotional and neutral pictures in the two experimental groups for the mPFC cluster which shows an effect of picture content, but no effect of experimental group.

The interaction effect was independent of the suspicion factor. The interaction of emotion and suspicion for the two exclusion groups revealed no activity in the above mentioned regions, even at a liberal significance threshold of $p < .01$ uncorrected.

There were no significant interactions between the factors group and social.

3.4. Reactivity to socio-emotional stimuli and aggressive behavior

For the emotional vs. neutral contrast-values averaged over those regions which showed a stronger reactivity to emotional stimuli in the exclusion group, we found positive correlations between aggressive behavior in the TAP and contrast values for the right middle frontal/precentral gyrus ($n = 34$; $r = .47$; $p = .005$; Fig. 5B) and the left inferior temporal gyrus ($n = 34$; $r = .38$; $p = .028$).

The mediational analysis showed that there was an indirect effect of social exclusion on aggression mediated by reactivity to emotional stimuli in the precentral gyrus (unstandardized effect size $b = 0.71$; SE = .41; lower and upper limits of the bias corrected confidence interval: 0.04 and 1.66). The indirect effect was non-significant when estimated for the fusiform ROI ($b = 0.21$; SE = .28; lower and upper limits of the bias corrected confidence interval: −0.32 and 0.82). We chose the directionality assumed by the model based on the theoretical assumption that effects of exclusion on neural processing should precede effects on behavior. However, due to the practical reasons mentioned above, this was not the temporal order at which the data were collected (behavioral data were collected prior to neural data). To ensure that a model adhering to the temporal order of the experiment would not explain our data better, we also tested whether exclusion had an indirect effect on reactivity of the precentral gyrus, mediated by aggressive behavior. This model showed no significant indirect effect ($b = 0.08$; SE = .09; lower and upper limits of the bias corrected confidence interval: −0.03 and 0.34).

4. Discussion

We investigated changes in the neural processing of socio-emotional stimuli as a possible mediator of the relationship between social exclusion and aggressive behavior. To this end, we combined a social exclusion paradigm, the cyberball game, with a behavioral measure of aggression and an fMRI-paradigm designed to measure the neural response to socio-emotional stimuli. Although we found no direct effect of social exclusion on aggression, social exclusion modulated the neural response to emotional stimuli, which was in turn related to aggressive behavior. A mediator analysis confirmed that there was an indirect effect of social exclusion on aggression, mediated by neural reactivity to socio-emotional stimuli.

4.1. Social exclusion and aggression

Contrary to previous studies (DeWall, Twenge, et al., 2009; Twenge et al., 2001), we found no direct effect of social exclusion on aggressive behavior in the TAP. However, we did find an increase in aggression for those participants, who believed that their game partners had excluded them on their own accord and had not been instructed to do so. Although this finding is based on small sample sizes and must therefore be interpreted cautiously, it indicates that the behavioral reaction to social exclusion depends on the victim's interpretation of the context in which the exclusion occurred.

These results are supported by our finding that non-suspicious excluded participants selected unprovoked, high punishments (6, 7 or 8) more often than suspicious or included participants. Thus, the exclusion experience alone was sufficient for eliciting aggression at a level that cannot be explained by provocation during the TAP.

An open question is whether exclusion has similar effects on provoked aggression. In a provocative TAP setting, exclusion and provocation might interact to further increase aggressive behavior, or the effect of provocation might diminish the effect of exclusion, increasing aggression in excluded and included participants alike. There is some evidence for the latter hypothesis (Bushman, Baumeister, & Phillips, 2001), but with the current study, we cannot answer this question.

4.2. Neural response to socio-emotional stimuli

In reaction to pictures of negative valence, we found increased activity in mPFC, STG, MTG, and IFG, which is in accordance with previous findings (Brunnlieb, Münte, Tempelmann, & Heldmann, 2013; Krämer et al., 2010; Sebastian et al., 2011; Singer, 2008; Ye et al., 2011), reflecting increased mentalizing processes during the observation of negative social scenes. Social exclusion was associated with increased reactivity of bilateral precuneus, STG, MTG, inferior temporal gyri and right middle frontal/precentral gyrus to emotional stimuli. Precuneus, MTG and STG are typically considered part of the mentalizing network, and are specifically associated with cognitive ToM (Lieberman, 2007; Saxe & Powell, 2006).

The cluster in the middle frontal/precentral gyrus for which we observed an interaction effect is part of the dorsal premotor cortex. Although this area is not typically mentioned as part of the mentalizing network, it is considered part of another network associated with perspective taking: the mirror neuron system (Montgomery & Haxby, 2008; Van Overwalle, 2009).

The mirror neuron system consists of a number of brain regions found to be activated during the performance of movements as well as the observation or anticipation of another person's motor actions and the inference of action goals and intentions (Bonini & Ferrari, 2011; Fabbri-Destro & Rizzolatti, 2008). Although the mentalizing and mirror neuron networks are mostly investigated separately, it has been suggested that both systems perform distinct functions, but are simultaneously recruited for action understanding (de Lange, Spronk, Willems, Toni, & Bekkering, 2008; Schippers, Gazzola, Goebel, & Keysers, 2009). Supporting this argument, Zaki, Weber, Bolger, and Ochsner (2009) found a positive relationship between accuracy of judgments of other's emotional state and activity in both mentalizing (mPFC, superior temporal sulcus) and mirror neuron (right inferior parietal lobule, bilateral dorsal premotor cortex) systems. Our results support the simultaneous recruitment of mentalizing and mirror neuron networks during the processing of socio-emotional stimuli. Both the inclination for taking the perspective of another person in distress, associated with cognitive mentalizing structures, and the inference of action goals, associated with the mirror neuron system, appear to be enhanced by social exclusion.

This finding is somewhat contradictive to the results of Powers et al. (2011), who found decreased reactivity of another region associated with the mentalizing network, the mPFC, to negative social stimuli in participants who had received an exclusion manipulation. Independent of exclusion, we did find increased activity in the mPFC for emotional compared to neutral pictures. Thus, emotional reactivity to negative social stimuli was not generally reduced in included participants but rather, excluded participants showed increased reactivity specifically for precuneus, premotor and temporal regions. It has to be noted that the method for social exclusion used by Powers et al., the future alone paradigm, is very different from the cyberball game we used. For one thing, participants in the study by Powers et al. did not experience an actual event of social exclusion. Furthermore, while the future alone paradigm predicts loneliness as a consequence of stable personality factors, participants in our study were given no reason to expect that social exclusion would occur in the future. Thus, the expectations participants had for future social interactions and the subsequent processing of socio-emotional stimuli may well differ between the two methods of social exclusion.

In their study combining cyberball and the TAP, Chester et al. (2013) investigated the relationship between aggression and increased activity in the dACC and anterior insula as indicators of negative affect during the exclusion experience itself and how this relationship is moderated by executive functioning. Our results, on the other hand, describe the changes in information processing following the exclusion experience, thus addressing the mediating processes between exclusion and aggression. While exclusion is likely a negatively valenced experience, our results specifically point toward changes in cognitive mentalizing processes following exclusion. Overall, it seems that social exclusion in our study led to an enhancement of cognitive mentalizing processes and to increased effort for understanding the actions and intentions of people depicted in distressing situations.

One has to note that we only used neutral and negative stimuli, as these have been sufficiently established in previous studies. Due to this limitation, we cannot say at this point, whether changes in mentalizing processes due to social exclusion are specific for negative emotional stimuli or generalize to emotional stimuli of different valence.

For the comparison of social and non-social pictures, we observed increased activity in occipital and parietal areas as well as the STG and MTG, which is consistent with previous findings (Krämer et al., 2010) and probably reflects increased visual input as well as processing of more complex scenes involving social relations. These effects were not modulated by social exclusion, indicating that the effect of exclusion on social information processing is specific for stimuli that contain some affective value and does not generalize to the basic processing of social stimuli per se.

4.3. Reactivity to socio-emotional stimuli and aggression

The increased reactivity of the right middle frontal/precentral gyrus and left inferior temporal/fusiform gyrus to emotional stimuli was found to be positively associated with aggressive behavior during the TAP. While there was no direct effect of exclusion on aggression, there was an indirect effect mediated by reactivity of the precentral gyrus to emotional stimuli. Thus, whether or not participants showed a behavioral effect of exclusion depended on how strongly exclusion affected their neural processing.

Our results indicate that increased cognitive mentalizing processes were associated with increased aggression. Generally, competence in Theory of Mind or empathy tasks is assumed to be negatively related to anger and aggression (Day, Mohr, Howells, Gerace, & Lim, 2012; Lovett & Sheffield, 2007). However, there is also some evidence for the reverse relationship in children, such that high cognitive ToM-skills are associated with increased proactive aggression (Renouf et al., 2010).

It should be noted that in the version of the TAP we used, participants were confronted with opponents who acted ambiguously and did not provoke aggressive behavior by selecting high punishments. Thus, aggression in this non-provocative version of the TAP was more proactive in nature than the aggression elicited by the typical TAP settings (Krämer, Buttner, Roth, & Münte, 2008; Krämer, Jansma, Tempelmann, & Münte, 2007), and may thus be positively related to cognitive ToM. Possibly, participants who showed more implicit cognitive mentalizing in response to negative social scenes attributed more hostile intentions to their opponents during the TAP.

This interpretation is in line with the relatively strong positive relationship between punishment selection in the TAP and the hostility subscale of the AQ of $r = .49$. For comparison, using a provocative TAP design and an alcohol manipulation, Giancola and Parrott (2008) found a positive relationship between hostility measured using the AQ and punishment selection of $r = .15$. They also found a positive relationship between physical aggression and punishment selection of .29, whereas these variables were unrelated in our study. This suggests that the tendency to attribute hostile intentions to other people apparently had a stronger influence on punishment selection in our experimental design than has been observed using a provocative TAP design.

Overall, our results are in agreement with findings of DeWall, Twenge, et al. (2009), who showed that hostile cognitive bias mediates the link between social exclusion and aggression. However, since our findings are based on correlational analyses, caution is warranted with causal interpretations. In future studies, this relationship could be investigated more closely by directly assessing the attributions made during the TAP.

4.4. Limitations

The high number of participants who were suspicious of the co-players' motivation for excluding them is an important limitation that has to be kept in mind when interpreting these results. In future studies, using different designs for the exclusion condition (such as opting for non-total exclusion or shortening the mutual inclusion at the beginning) might be useful, although each design comes with its own merits as well. Our results suggest that exclusion has substantial general effects on neural processing independent of the attributions made by the victim, but that external attribution can support non-aggressive behavior. While this divergence between neural and behavioral effects presents as an interesting finding in itself, however, it also constitutes a possible confound in the relation between neural and behavioral effects, which at this point of research, we cannot fully resolve.

5. Conclusions

In conclusion, our findings suggest that social exclusion leads to changes in the neural processing of socio-emotional stimuli, as previously shown on a behavioral level (DeWall, Twenge, et al., 2009). Exclusion led to increased recruitment of areas associated with perspective taking and action goal inference in response to negative social stimuli. Reactivity of brain areas associated with these cognitive ToM processes, in turn, was positively related to proactive aggressive behavior during the subsequent competitive reaction time task.

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