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Behavior and Neural Correlates of Empathy in Adolescents

Sandy Overgaauw[a, b] Berna Güroğlu[a, b] Carolien Rieffe[a] Eveline A. Crone[a, b]

[a]Department of Psychology, and [b]Leiden Institute for Brain and Cognition, Leiden University, Leiden, The Netherlands

Key Words
Empathy · Social interaction · Adolescence · fMRI data analysis · Prosocial behavior · Dictator game

Abstract
This study examined neural correlates of empathy in adolescence while observing harmful acts. A total of 32 participants (aged 12–19 years) viewed pictures depicting negative (offenders inflicting intentional harm) and positive (friends socializing) social situations. After viewing each picture, participants could allocate hypothetical points to either the offender or the victim in a dictator game. Behaviorally, participants of all ages acted prosocially towards victims, fairly towards positive individuals and punishingly towards offenders. Brain imaging analyses showed that viewing negative situations was associated with more activation in the bilateral intraparietal lobule and the superior temporal sulcus (STS), whereas viewing positive situations was associated with more medial prefrontal cortex and left temporal parietal junction activity. Analyses testing for associations between brain activity and self-reported empathy showed that the STS was correlated negatively with reports of understanding others' distress and the willingness to help others. Together, the findings suggest that adolescents show similar prosocial behavior, as previously reported in adults with greater STS activity, when observing negative social acts that is modulated by an individual's empathy for others.

Introduction

Adolescence is marked by pronounced social-cognitive and social-affective changes, requiring the acquisition of new social skills and providing new challenges with important repercussions for the development of social relationships [1]. An important component for behaving adequately in response to others' emotions and behavior is empathy. Empathy is often defined as the ability to feel and read (affective) mental states of others, which helps us to understand and predict their intentions [2, 3]. In childhood and adolescence, empathic skills play an important role in how children and adolescents act toward individuals in their social group. For example, children who report higher empathic skills are better able to regulate their emotions and act in more prosocial ways towards others [4–6]. The current study aimed to investigate the neural underpinnings of individual differences in empathic concern in adolescence in the evaluation of

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Sandy Overgaauw
Department of Developmental Psychology
Wassenaarseweg 52
NL–2333 AK Leiden (The Netherlands)
E-Mail s.overgaauw.2@fsw.leidenuniv.nl

intentional negative social situations involving offenders and victims.

Empathy has previously been described as consisting of the following three components: (1) affective empathy, defined as the capability to identify with another person's emotions, (2) cognitive empathy, defined as the ability to understand these emotions and reason about affective states, and (3) mentalizing, which refers to the ability to reason about cognitive states [7, 8]. The latter component provides an important mechanism that enables us to differentiate between one's own and others' feelings. To put it briefly, empathy empowers us to feel and understand others' emotions, and provides us with a regulatory system to counteract possible overarousal resulting from such an empathic reaction [9].

Previous neuroimaging studies have suggested that mentalizing is specifically linked to the medial prefrontal cortex (mPFC), an area that has been found to be crucial for social information processing. Studies on people with a lesion in this brain area have shown that these patients were not able to read others' mental states based on nonverbal cues [10, 11] and neuroimaging studies report that this region is consistently engaged in mentalizing tasks [12]. In addition, neuroimaging studies showed that the superior temporal sulcus (STS), the temporal parietal junction (TPJ) and the intraparietal sulcus (IPS) are involved in processing intentional and goal-directed behavior of others [13–15]. For example, Kramer et al. [7] found that when interpreting dyadic interactions with empathic content, there was increased activation in the STS, but not in single-person situations, indicating the important role of the social context.

Furthermore, mentalizing areas are differentially sensitive to observing positive and negative social situations. That is to say, it was previously found that observing pain was associated with increased activation in the IPS and STS, whereas observing happy scenarios was associated with increased activation in the mPFC and TPJ [16]. The mPFC is thought to code the emotional value of social display, as this region is more engaged when viewing social situations with more positive valence ratings [17]. In other words, neural regions involved in observing social scenarios seem to be differentially sensitive to negative (e.g. harmful or painful) and positive (e.g. happy) social events.

Developmental neuroimaging studies have suggested that the transition from an egoistic form of empathy in young children to a more reciprocal concern for other people in adulthood [18, 19] is driven by the development of brain areas which support mentalizing [20, 21]. For example, it was previously shown that bilateral TPJ was more active in response to different mental states in adults compared to children [22, 23]. In addition, several studies showed that during adolescence this network of mentalizing areas (TPJ, STS, mPFC) becomes increasingly active when reasoning about complex social emotions [27] or incorporating intentionality of others into decision making [25, 26]. These studies lead to the hypothesis that brain regions associated with empathy-related mentalizing develop during adolescence. Given that cognitive empathic skills increase during adolescence [28], an important question concerns whether individual differences in empathic ability predict neural activity associated with empathy-related mentalizing.

In the present study we examined neural responses in adolescence when viewing pictures of negative and positive social situations and how these responses relate to self-reported levels of empathy. We were specifically interested in neural responses when viewing negative social situations in which a person intentionally inflicts pain on someone else (attention directed to either the victim or the offender) and positive social situations (attention directed to one of the happy people). Using this manipulation, we tested whether regions in the mentalizing network (TPJ, STS, mPFC), that are known to develop during adolescence, were differentially sensitive to the perception of negative or positive social situations. It is currently unknown whether higher levels of empathy are related to enhanced activity in the mentalizing brain areas such as the mPFC, TPJ, STS and IPS due to increased mentalizing capacities (i.e. related to a higher degree of 'feeling' for the other) or due to a better ability to down-regulate empathic responses (i.e. related to better self-other differentiation and regulation).

Following Decety et al. [29], we tested whether participants differentiated between the agents in harmful and positive social events by examining subsequent punishing behavior. Decety et al. previously examined punishment behavior of children, adolescents and adults (aged 4–37 years) after observing harmful events. They found milder punishment with increasing age of agents who intentionally harmed a person. Based on these findings, participants played a hypothetical dictator game after observing harmful acts. The dictator game involves transfer to or sharing of money with others. Specifically, participants played dictator games with agents who harmed others, were being harmed, or were present in a positive social event. We predicted that less money would be allocated to offenders compared to victims or people in a positive social situation [29]. This manipulation was used to validate that participants differentiated between social conditions.

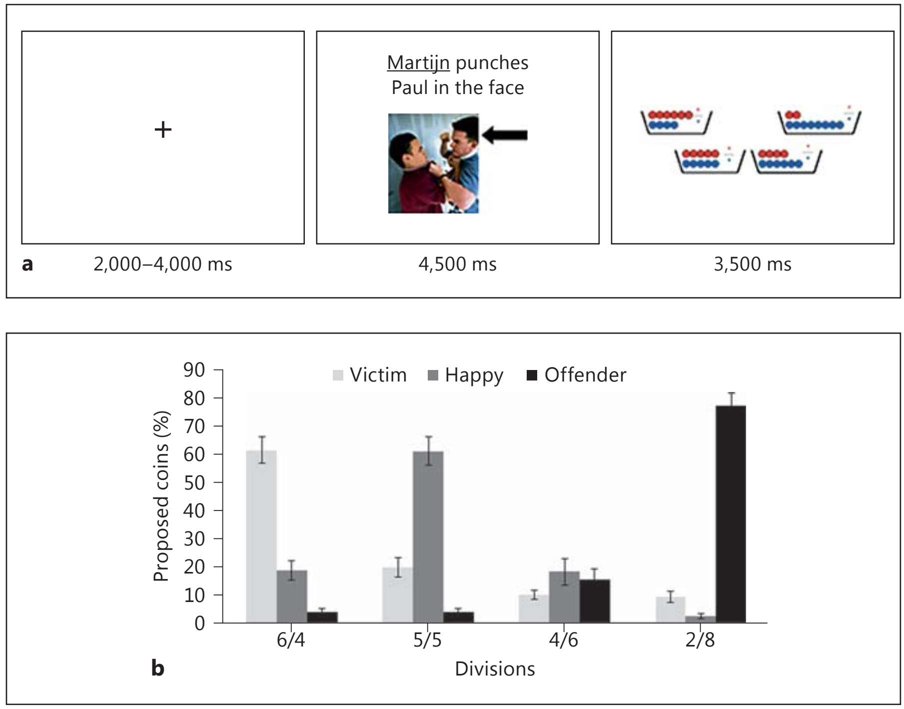

Fig. 1. a Task display. Each trial consisted of a stimulus presented for 4.5 s followed by a dictator screen presented for 3.5 s. The stimulus could be a harmful act by an offender, a harmful act to a victim or a positive stimulus. The dictator game requires an allocation choice out of 4 options (see text for explanation). **b** Percentage allocated coins to an offender, a victim or a positive person.

Methods

Participants

In total, 37 right-handed and typically developing adolescents between the ages of 12 and 19 years participated (mean age = 15.5, SD = 2.09, 14 males and 23 females). Initially, we contacted 50 participants who were in the database for individuals who expressed willingness to participate in research; 13 of these participants could not participate due to braces, a clinical diagnosis or because they did not respond to our calls and/or e-mails. From the 37 participants who participated in the scanning session, we excluded data from 5 participants due to movement (>3 mm, n = 4) or incomplete data (n = 1); this resulted in a final sample size of 32 participants. Participants were recruited from different secondary schools and through our subject recruitment database. Parents of adolescents under 18 years of age and participants over 18 were asked to give written consent. After participation, participants received a monetary incentive. The institutional review board of the university medical center approved all procedures before the start of the study.

Experimental Task: Empathy-Dictator Game

Participants performed an empathy-dictator game (EDG), in which they were presented with social situations involving individuals involved in a negative or a positive social situation. Following Decety et al. [29], we tested whether participants differentiated between the agents in negative and positive social situations by examining subsequent punishing behavior. After viewing each situation, they were asked to distribute coins between themselves and another person depicted in the social situation. In a dictator game, the participant decides how to divide a certain stake (e.g. coins) between themselves and another player, thereby making a balance between concern for one's own gain and concern for others. The current study used a modified dictator game that allowed us to examine whether participants differentiated between victims and offenders in their evaluation of harmful acts. In the current version of this coin distribution game the participants were given four fixed distributions of coins as options where they could choose from rather than allowing them to make a choice of 1–10 coins. We predicted that less money would be allocated to offenders compared to victims or persons in positive situations [29].

The social situations showed either negative social situations (involving inflicting intentional harm on another person) or positive social situations. In the harmful social situations, participants were asked to either focus on the offender or on the victim. Thus, three conditions were created (negative offender, negative victim, positive happy person). Each condition consisted of 15 stimuli and these were presented in a random order. Fifteen adults, who were asked to score the different situations on how harmful they were, validated the 45 stimuli beforehand. Each situation contained at least 2 people of the same age group as the participant. A brief sentence describing the event was shown on the screen below the picture. The person with whom the participant was asked to share coins was indicated with an arrow pointing to him/her. Even though there were only positive social interactions in the positive condition, an arrow was inserted also in these conditions, pointing at 1 of the individuals in the picture in order to balance processing demands related to the arrow. In short, the person indicated by the arrow was either a victim, an offender or a person with positive affect (fig. 1).

Prior to the presentation of each stimulus, a jittered fixation-cross appeared for a duration between 2,000 and 4,000 ms. Subsequently, the stimulus was presented for 4,500 ms. After the stimulus, a selection screen was shown with four options to divide coins:

a prosocial offer (6/4; 6 coins for the other and 4 coins for the participant), an equal offer (5/5), an offer that is slightly more advantageous for the participant (4/6) and an unfair offer (2/8). This screen was presented for 3,500 ms, during which the response was made. In case participants did not respond within this time window, a screen with the message 'Too late' was displayed. This occurred in less than 2% of the trials, which were further discarded from the analyses.

Behavioral Measures: The Empathy Questionnaire

Participants completed 18 items of the Empathy Questionnaire (EmQue. [30]), a self-report with three scales: contagion (7 items), which refers to affective empathy (e.g. When a friend is upset, I feel upset too), understanding (5 items), which reflects cognitive empathy (e.g. When a friend is angry, I tend to know why) and support (6 items), which reflects the tendency to act prosocially (e.g. If a friend is sad, I want to do something to make it better). Answers could be given on a 3-point scale: (1) not true, (2) sometimes true and (3) often true. All 18 questions were formulated positively, with higher scores reflecting higher empathic abilities. Mean scores were computed and used for the analyses (minimum score = 1, maximum score = 3). Scores on all three scales were normally distributed, with skewness as follows: 0.27 (SE = 0.414) for contagion, −1.02 (SE = 0.414), for understanding, 1.02 (SE = 0.414) and −1.93 (SE = 0.414) for support. Cronbach's alphas of the three scales of the EmQue. were as follows: contagion: 0.73, understanding: 0.64, and support: 0.75.

fMRI Data Acquisition

E-prime software (Psychology Software Tools, Inc., Pittsburgh, Pa., USA) and a rear projection system were used for the stimuli presentation. Scanning was performed using a 3-tesla Philips Achieva scanner at the Leiden University Medical Center. Functional data were acquired using T2*-weighted echo-planar images (TR = 2.2 s, TE = 30 ms, slice-matrix = 80 × 80, FOV = 220, 35 transverse slices of 2.75 mm with 0.28-mm gap) during one functional run of 259 volumes. The first 2 volumes of this run were discarded to allow for equilibration of T1 saturation effects. After the functional scanning, high-resolution T2*-weighted images and high-resolution T1 anatomical images were obtained.

fMRI Data Analysis

Image processing was carried out with SPM8 (Welcome Department of Cognitive Neurology, London, UK). For each participant, the T1-weighted image was segmented and spatially normalized using the default parameters. The fMRI data were corrected for motion, coregistered with the T1 anatomical image and normalized to a T1 template. Templates were based on the MNI305 stereotaxic space [31]. The normalization algorithm used a 12-parameter affine transformation together with a nonlinear transformation involving cosine basic functions, and resampled the volumes to 3-mm cubic voxels. Data were then spatially smoothed with an 8-mm FWHM isotropic gaussian kernel. Due to excessive head movement, 4 participants were excluded. The remaining participants did not exceed 1 voxel (<3 mm) in any direction for any scan. Mean and maximum head movement was 0.1 and 2.91 mm. Images were corrected for differences in timing of slice acquisition, followed by rigid body motion correction.

Statistical analyses were performed on group data using a random-effects model using one-sample t tests. The fMRI time series data were modeled by a series of events convolved with a canonical hemodynamic response function. The modeled events based on correctly performed trials were used as covariates of interest in a general linear model along with a basic set of cosine functions that high-pass filtered the data. The least-squares parameter estimates of height of the best-fitting canonical hemodynamic response function for each condition were used in pair-wise contrasts. The presentation of the social situation and the presentation of the decision screen were modeled as zero-duration impulse functions. Trials on which participants did not respond within the 3,500-ms time frame (i.e. too late screen) were not included in the contrasts of interest. The first-level analyses were group averaged at the second level and further analyzed using one-sample t tests. Activation related to processing negative and positive social situations were examined by contrasting negative social situation > positive social situations and vice versa. Activation related to empathy for processing of harmful acts was examined by focusing on two contrasts: trials where the arrow pointed at the offender versus positive situations (offender > positive) and trials where the arrow pointed at the victim versus positive situations (victim > positive). To test for differences in neural responses to offenders versus victims, we examined the contrasts offender > victim and victim > offender.

We used the MarsBar toolbox in SPM8 [32] to perform region of interest (ROI) analyses to further investigate patterns of activation for the three conditions and to correlate neural activation with the self-report scales for empathy and average prosocial behavior on the empathy-dictator game. ROIs were defined based on functional masks of the whole-brain analyses (FWE corrected, $p < 0.05$, at least 10 contiguous voxels) and were averaged across all the voxels in the cluster, resulting in a mean value per ROI for each condition for each participant. All brain coordinates are reported in MNI atlas space.

Results

Self-Reported Empathy

Mean scores on the scales of the EmQue. are: contagion: 2.21 (SD = 0.41), understanding: 2.54 (SD = 0.36), and support: 2.58 (SD = 0.42).

Empathy-Dictator Game

As can be seen in figure 1b, participants differentiated between the offender, the victim and the person in the positive situations in their allocation of coins. The 3 (person) × 4 (choice) repeated-measures ANOVA resulted in the expected person × choice interaction ($F_{1, 32} = 366.85$, $p < 0.001$; $\eta^2 = 0.92$). The most frequent allocation for the positive person was an equal (5/5) distribution of coins (mean = 60.85%), whereas the most frequent allocation for the victim was a prosocial (6/4) distribution (mean = 61.18%) and an unequal (2/8) distribution for the offender (mean = 77.07%). These findings confirm that participants clearly differentiated between the different conditions.

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fMRI Results: Whole-Brain Contrasts

We first examined the contrasts offender > victim and victim > offender in order to investigate differences in neural activation when focusing on offenders versus victims in observing a social situation. These contrasts yielded no differences in neural activation, thus these two conditions were combined as a 'negative situation' condition.

Next we examined the negative situation > positive situation and the reversed contrasts. The negative situation > positive situation contrast resulted in more activation in the right STS (RSTS: 51, –57, 6), the left STS (LSTS: –51, –60, 6), the right inferior parietal lobule (RIPL: 63, –30, 33) and the left inferior parietal lobule (LIPL: –57, –33, 24) when observing negative acts (fig. 2). The reverse contrast of positive situation > negative situation resulted in increased activation in the mPFC (–3, 57, 3) and left TPJ (LTPJ: –42, –69, 30; fig. 3). The coordinates of all peak activations in both contrasts are reported in table 1.

Table 1. All brain coordinates based on the whole-brain contrasts negative situation > positive situation and positive situation > negative situation

Contrast region	MNI (x, y, z) coordinates	Z value	Volume (= k_E value in SPM)
All participants: negative > positive			
LSTS	–51, –60, 6	6.96	213
RSTS	51, –57, 6	5.66	23
LIPL	–57, –33, 24	6.14	91
RIPL	63, –30, 33	5.58	28
Precuneus	24, –81, 39	5.93	19
All participants: positive > negative			
mPFC	–3, 57, 3	5.81	100
LTPJ	–42, –69, 30	5.64	33
Hippocampus	–24, –21, –18	5.68	11
Cingulate gyrus	0, –45, 36	5.58	34

FWE corrected, p < 0.05, 10 contiguous voxels. LSTS = Left superior temporal sulcus; RSTS = right superior temporal sulcus; LTPJ = left temporal parietal junction.

fMRI Results: Connection Behavior and Neural Activation

To test whether there was a relationship between neural activity for negative situation > positive situation to subsequent behavior in the dictator game, an average prosocial offer score (positive outcome for responder) was created by averaging across the percentage chosen 6/4 and 5/5 divisions for each condition (offender, victim, happy person) separately. Subsequently, a correlation analysis with neural activity in the four ROIs extracted from the contrast negative situation > positive situation (LSTS, RSTS, LIPL, RIPL) and average prosocial offer scores, separately for each condition (offender, victim, happy person), showed that the R was negatively related to subsequent prosocial scores when dividing coins with offenders ($r = –0.35$, $p < 0.05$, not Bonferroni corrected). Thus, more RIPL activity was associated with less prosocial and more punishing behavior. The other correlations were not significant.

Similar correlation analyses with neural activity in the two ROIs extracted from the contrast positive situation > negative situation (mPFC, LTPJ) and average prosocial and antisocial offer scores showed no relationship between the frequency of prosocial or antisocial offers and neural activity in mPFC or LTPJ.

fMRI Results: Self-Reported Empathy Analysis

Next we examined the relation between neural activation in the same ROIs extracted from the whole-brain analyses (bilateral STS, bilateral IPL, mPFC, LTPJ) and empathy. For this purpose, we performed correlation analyses between the difference scores for the negative situation > positive situation and scores on the empathy scales. There was a negative correlation between neural activation in LSTS (for negative situation > positive situation) with empathic understanding ($r = –0.40$, $p < 0.05$) and support ($r = –0.47$, $p < 0.01$), but not for contagion. Thus, adolescents who reported a better understanding of others' distress and who were more willing to help showed less activation in the LSTS during negative social interactions (involving intentional harm), whereas adolescents who reported lower levels of understanding and support showed more activation in LSTS for negative social interactions (fig. 4). There were no other correlations found. See table 2 for correlations among the three scales.

Discussion

In the current study we investigated neural activation in response to viewing negative and positive social situations during adolescence. Specifically, we tested which neural regions were sensitive to witnessing harmful acts and how these patterns of brain activity were related to social behavior and self-reports of empathy. The behavioral results showed that participants treated others differentially during the empathy-dictator game depending

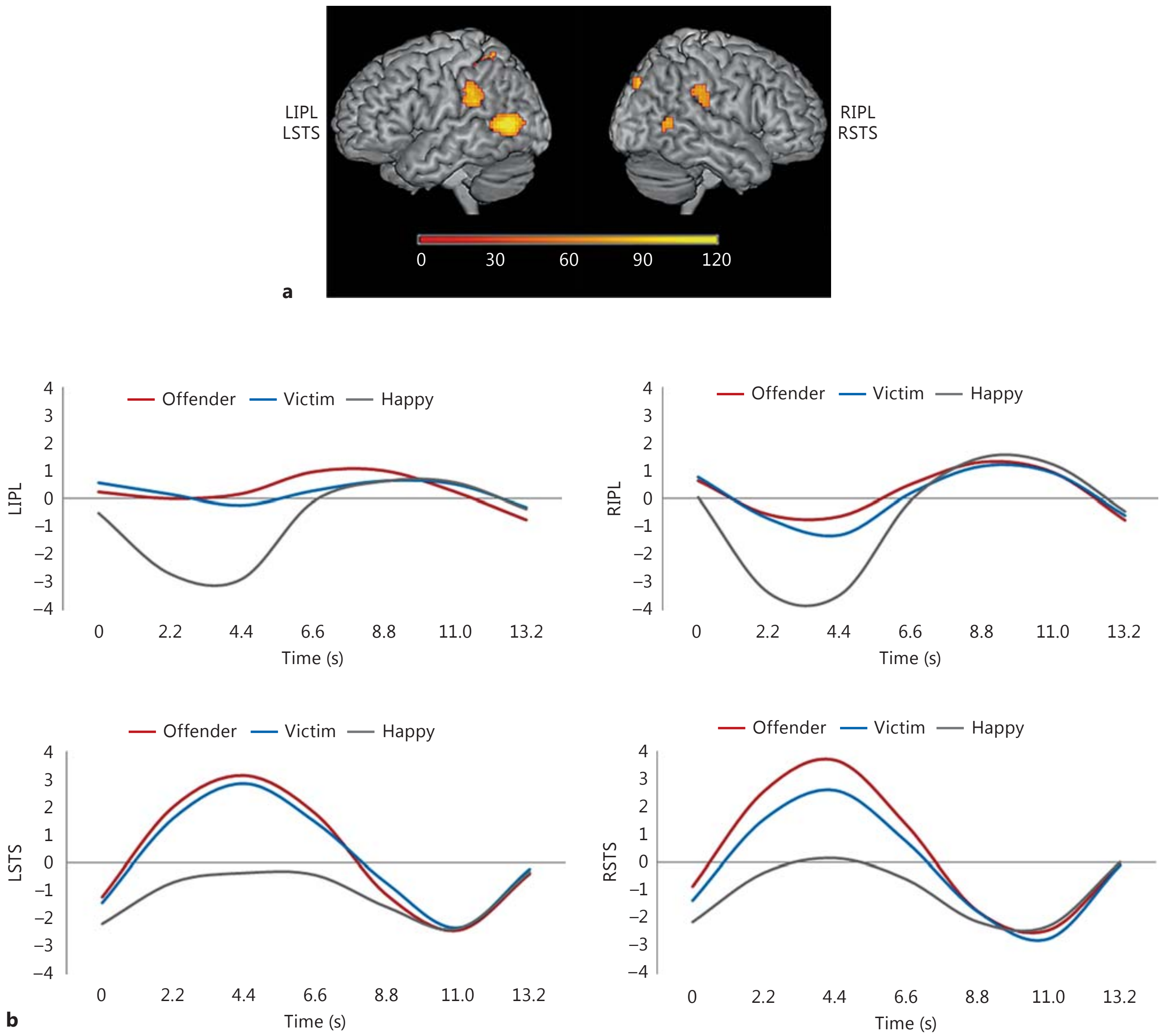

Fig. 2. a Neural responses in the contrast negative situation > positive situation showing activation in bilateral IPL and bilateral STS (FWE corrected at $p < 0.05$, at least 10 contiguous voxels). **b** Time series for bilateral IPL and bilateral STS. The colored horizontal bar represents the t values. For the coordinates, cluster sizes and statistical values for each active cluster we refer to table 1. The time series are presented in TRs of 2.2. s, where 0 marks the onset of the stimulus presentation. Note that the activation pattern in IPL is showing deactivation at the onset of stimulus presentation, which is not uncommon for social mentalizing areas [16, 27]. LSTS = Left superior temporal sulcus; RSTS = right superior temporal sulcus.

on the preceding social behavior of the person: they acted more prosocially toward victims, more punishingly toward offenders and more fairly toward persons involved in positive social situations. These behavioral findings indicate that empathy in the evaluation of negative social situations, involving intentionally harmful acts and harmed victims, is present in adolescents [29, 33, 34].

Brain regions in the mentalizing network (TPJ, STS, mPFC) were examined to determine whether they were more active when observing negative (harmful) relative

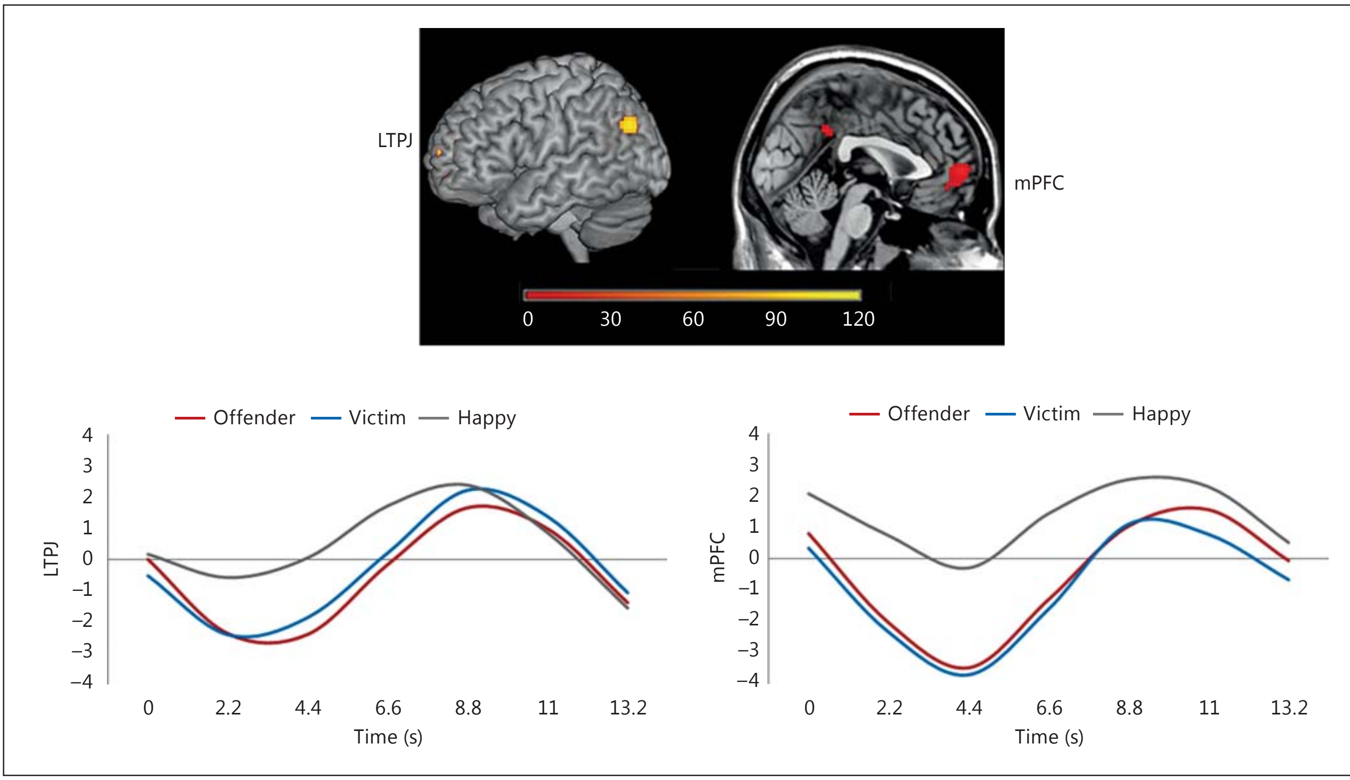

Fig. 3. a Neural responses in the contrast positive situation > negative situation showing activation in the mPFC and LTPJ (FWE corrected at $p < 0.05$, at least 10 contiguous voxels). **b** Time series for vmPFC and LTPJ. The colored horizontal bar represents the t values. For the coordinates, cluster sizes and statistical values for each active cluster we refer to table 1. The time series are presented in TRs of 2.2. s, where 0 marks the onset of the stimulus presentation. Note that the activation pattern in vmPFC and TPJ is showing deactivation at the onset of stimulus presentation, which is not uncommon for social mentalizing areas [27]. LTPJ = Left temporal parietal junction.

Table 2. Correlations between the 6 task-related ROIs and the scales of the EmQue. and age

	RSTS	LIPL	RIPL	mPFC	LTPJ	Contagion	Understanding	Support	Age
Negative > positive									
LSTS	0.64**	0.48**	–0.62	–0.16	0.60**	–0.08	–0.40*	–0.47**	–0.21
RSTS		0.39**	0.39*	–0.31	–0.20	–0.11	–0.17	–0.17	–0.34
LIPL			0.82**	–0.40	–0.09	–0.31	–0.34	–0.29	–0.13
RIPL				–0.20	0.06	–0.13	–0.18	–0.18	–0.16
Positive > negative									
mPFC					0.60**	–0.13	–0.07	–0.18	0.34
LTPJ						–0.13	–0.15	–0.00	0.11
EmQue.									
Contagion							0.35	0.52**	–0.22
Understanding								0.48**	–0.19
Support									–0.27

* $p < 0.05$, ** $p < 0.001$. LSTS = Left superior temporal sulcus; RSTS = right superior temporal sulcus; LTPJ = left temporal parietal junction.

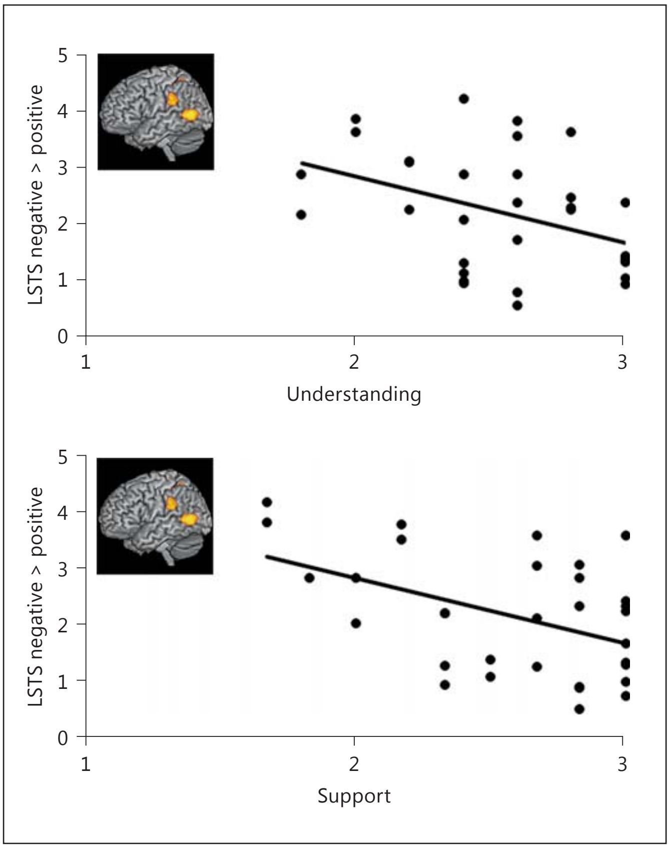

Fig. 4. Correlation between neural activation in LSTS for ROI values in the contrast negative situation > positive situation and self-reported empathic support and understanding – ROI based on whole-brain analyses for the main contrast negative situation > positive situation (FWE 0.05 corrected, at least contiguous 10 voxels; coordinates x = –51, y = –60, z = 6; see table 1). LSTS = Left superior temporal sulcus.

to positive social situations. The imaging findings showed that stimuli depicting victims and offenders were both associated with stronger activation in bilateral STS and IPL. These findings are consistent with prior studies showing that these regions are involved in predicting intentional behavior, perspective taking and mentalizing [35–37]. The STS has not been consistently found in all studies that showed physically painful situations [38–40]. Possibly, this region is sensitive to the context in which the harm-inflicting acts occur, as Kramer et al. [7] found that only in the case of dyadic interactions (as in the current study) increased STS activation was found. In the current study we draw attention to the actors in the situation by pointing an arrow and giving a short written explanation, which may have resulted in more mentalizing in social interactions involving intentional harm.

In order to investigate possible individual differences in neural responses to harmed (victims) or harming people (offenders) in the time span of adolescence, we related neural activation to individual differences in empathic traits. We focused on the domains of empathy: contagion (affective empathy), understanding (cognitive empathy) and support (tendency to act prosocial) as distinct predictors of empathy on neural activity. We found a negative correlation of LSTS activity when adolescents were looking at harmful acts and self-reports of empathic understanding and support. The higher the understanding- and support-related empathy skills the less STS activity – previously been shown to be involved in social perception [41]. This finding is consistent with previous work showing the involvement of the STS when taking ‘other perspective’ versus ‘self-perspective’ [37]. It is possible that adolescents with lower empathy skills are more involved in their own perception than in the other. The RIPL showed a similar effect, that is to say, more IPL activity when observing offenders was associated with less prosocial, more punishing, behavior, although this effect was weaker than the STS effect and did not survive correction for multiple comparisons. Taking these results together, the current results suggests that STS (and IPL) may be more involved in thinking about intentions when observing harmful acts and this effect is stronger in adolescents who report lower understanding and support [42]. In future research, it will be interesting to test these questions using connectivity analyses, as these analyses give information about communication between brain regions.

The reversed contrast of positive versus negative situations resulted in an increase in hemodynamic activity in the mPFC and LTPJ. This effect is consistent with a previous study of Morelli et al. [16], in which they found similar regional activity in adults when observing pictures of happy people relative to neutral pictures. Morelli et al. argued that individuals interpret physical pain by watching a person harming another, whereas situations with a more positive valence require evaluating the situation as a whole. Others have suggested that the ventral mPFC (vmPFC) tracks reward more generally based on social emotional stimuli [17]. Although the current results are in line with these previous findings, vmPFC activation has also been found when adults observed pictures of intentionally negative acts [29]. However, the paradigm used in these prior studies [29] contained pictures of only body parts without showing faces. Even though this effect was reported for negative situations, these stimuli could still make an appeal on the abilities to judge and evaluate a social situation [16]. Therefore, future studies are needed to clarify the role mPFC and TPJ play in evaluating social stimuli.

Contrary to prior studies, there was no consistent activation in the anterior cingulate cortex (ACC), insula and amygdala when observing harmful situations. ACC activation is often linked to affective rather than cognitive empathy (sympathizing with someone's pain and experiencing the pain yourself [43, 44]). One possibility is that playing the dictator game after each social situation caused participants to predecide while observing the social acts rather than only experiencing the primary impact of observing pain. Alternatively, this outcome could be explained by the stimuli used in the current study. The negative stimuli depict an intention for a harmful social act, whereas previous studies focused on the mirror system for experiencing pain and empathizing with pain experienced by another [40]. Future studies should focus on the role of the ACC in affective and cognitive components of empathy.

Some limitations of this study deserve further attention. First, the adolescents clearly differentiated in their sharing treatment of others depending on whether the other was a victim, an offender or a person involved in a positive social situation, and this behavior was consistent across trials. A disadvantage was that therefore it was not possible to compare social and antisocial responses following observation of the same social interactions (e.g. participants almost always punished offenders, therefore we could not investigate neural responses to treating the offender fairly). In addition, given that we used restricted choice options, the positive options (6/4 and 5/5) were less generous than the negative options (4/6 and 2/8), which could have primed participants to make more greedy choices. Second, the sample size was relatively small with an unequal division between boys and girls, which impacted our power to investigate the unique contribution of gender to empathic abilities. Considering developmental trajectories of girls (aged 13–18) scoring high on both affective and cognitive empathy [28], it would be interesting for future research to investigate to what extent empathic abilities are mediated by gender differences. Furthermore, it would be interesting to investigate the predictive role of age in combination with specific, context-dependent and individual empathic abilities for prosocial behavior. In order to detect age-related changes, future longitudinal studies should examine whether these relations are based on trait versus state characteristics and their stability patterns across adolescence [45].

Taken together, our findings highlight the involvement of social brain networks when observing negative (IPL and STS) and positive social situations (mPFC and TPJ) during adolescence. The neural correlates of empathy are important for understanding the mechanisms underlying the development of social behavior during this period [46]. Our findings emphasize an important role of individual differences in empathy at the social and neural levels of social cognition. Clearly, future studies that examine the impact of accidental harmful acts [2, 47, 48], gossiping or social exclusion [49] may further our understanding of empathy and social pain. The current study provides a first step in this direction.

Appendix A

Neural activation in the rostral ACC (3, 45, –3, 17 voxels, $Z = 3.84$) in the contrast negative situation > positive situation with the support subscale as regressor ($p < 0.001$ uncorrected, at least 10 contiguous voxels). No other clusters were detected for this contrast.

Appendix B

Neural activation in the dorsal ACC (–9, –12, 42, 10 voxels, $Z = 3.55$) in the contrast positive situation > negative situation with the support subscale as regressor ($p < 0.001$ uncorrected, at least 10 contiguous voxels). No other clusters were detected for this contrast.

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