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# Me or you? Neural correlates of moral reasoning in everyday conflict situations in adolescents and adults

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Throughout adolescence, progress in the understanding of the moral domain as well as changes in moral behavior is observable. We tested 16 adolescents (14–16 years of age) and 16 healthy adults (22–31 years of age) on the developmental changes in everyday moral decision making using functional magnetic resonance imaging (fMRI). Using verbal stories describing everyday moral conflict situations, subjects had to decide between a moral standard or a personal desire. In the moral conflict situations, adolescents not only chose significantly more often the hedonistic alternative than adults, but they also reported higher certainty ratings. Contrasted with everyday social conflict situations that required a decision between a social-oriented behavior and a personal need, moral conflict situations induced an activity increase in frontal areas, the middle temporal gyrus, the thalamus, and the parahippocampal gyrus in adolescents compared to adults. Moreover, a closer look at the moral conflict situations revealed that adolescents showed more activity than adults in brain areas that are also centrally involved in theory of mind (ToM) during morally oriented decisions in contrast to personal-oriented decisions. This indicated that the development of moral reasoning may be strongly correlated with the development of ToM reasoning.

***Keywords:*** Development; Adolescence; Moral reasoning; Morality; Theory of mind.

During adolescence, teenagers undergo a variety of interrelated changes, such as physical and hormonal changes associated with puberty, fundamental cognitive changes associated with the emergence of higher levels of intellectual abilities, and social changes associated with an increasing orientation to peer groups (Moshman, 2011). Adolescence is also characterized as the period in which individuals begin to explore themselves in order to discover who they are and how they can interact with the social world in which they live (Crone & Dahl, 2012; Steinberg & Morris, 2001). In order to form an identity, adolescents begin to explore possibilities, make commitments, and construct theories of themselves along several distinct dimensions, such as sexuality, gender, appearance, religion, academics, social relations, values, and morality (Moshman, 2011; Steinberg, 2005; Steinberg & Morris, 2001). Whereas in childhood the self is defined primarily in terms of nonmoral properties, such as appearance or behavior, in late adolescence as well as in adulthood, individuals define themselves in more psychological and social terms, where moral reasoning and moral behavior play important roles (Eisenberg, 2000; Eisenberg, Sheffield Morris, Mcdaniel, & Spinrad, 2009).

Progress in the understanding of the moral domain and changes in moral behavior is associated with advances in perspective taking skills (Eisenberg

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et al., 2009; Moshman, 2011) and with the developing understanding that peoples' behavior depends on what they know, wish, or intend irrespective of the real state of the world (Baird & Astington, 2004; Dumontheil, Apperly, & Blakemore, 2010; Dunn, Cutting, & Demetriou, 2000; Killen, Mulvey, Richardson, Jampol, & Woodward, 2011; Knobe, 2005; Krettenauer, 2004). Besides these behavioral and cognitive changes, recent research has documented that significant structural brain changes are observable through adolescence (Gogtay et al., 2004; Shaw et al., 2008; Sowell et al., 2004; Toga, Thompson, & Sowell, 2006). For example, Gogtay et al. (2004) measured changes in grey-matter density between 4 and 21 years of age and showed a functional maturation sequence. Within the frontal cortex, the precentral gyrus matures early and the prefrontal cortex matures last. In the parietal lobe, the grey-matter loss begins in the postcentral gyrus and progresses laterally into the angular gyrus and supramarginal gyrus. In a longitudinal study, Shaw et al. (2008) investigated the cortical thickness of children and young adults between 3 and 33 years of age and found neurodevelopmental trajectories closely related to their laminar architecture for different brain areas. Whereas cortical regions with simple laminar architecture, such as limbic areas, show a simple linear growth, polysensory and higher-order association areas of the cortex have more complex trajectories. (Shaw et al., 2008). In addition to revealing grey-matter changes, research shows that structural maturation of white matter also continues during adolescence, as reflected in developmental changes in its volume and in its microstructure (Paus, 2010; Schmithorst & Yuan, 2010).

Neuroimaging studies that investigated the neural correlates of moral reasoning have revealed that those brain areas that undergo significant developmental modulation during adolescence are also critically involved in moral reasoning (Bzdok et al., 2012; Casebeer, 2003; Moll, Zahn, de Oliveira-Souza, Krueger, & Grafman, 2005). These studies investigated either judgments about morally salient claims (e.g., "The elderly are useless"; Moll, de Oliveira-Souza, Eslinger, et al., 2002), ethical moral dilemmas (e.g., stealing one person's organs in order to distribute them to five others; Greene, Sommerville, Nystrom, Darley, & Cohen, 2001), or the transgression of moral norms (e.g., "You crash into another car and kill the passenger"; Berthoz, Armony, Blair, & Dolan, 2002; Finger, Marsh, Kamel, Mitchell, & Blair, 2006; Young & Saxe, 2008). For adults, these studies indicated that moral decisions are associated with increased activity in the lateral and medial frontal cortex, the anterior temporal cortex, the anterior cingulate cortex and limbic structures such as the thalamus and the amygdala (Casebeer, 2003; Greene & Haidt, 2002; Moll et al., 2005).

Whereas a growing number of studies investigated the neural correlates underlying the developmental changes in social understanding (Blakemore, Den Ouden, Choudhury, & Frith, 2007; Burnett, Bird, Moll, Frith, & Blakemore, 2009) and theory of mind (ToM) (Kobayashi, Glover, & Temple, 2007; Liu, Sabbagh, Gehring, & Wellman, 2009; Meinhardt, Sodian, Thoermer, Döhnel, & Sommer, 2011; Sommer, Meinhardt, et al., 2010), there are only a few studies that have examined the neural basis of moral reasoning in the developing brain (Decety, Michalska, & Kinzler, 2012; Harenski, Harenski, Shane, & Kiehl, 2012; Pujol et al., 2008). Pujol et al. (2008) investigated teenagers between 14 and 16 years of age. They specifically focused on the activity of the posterior cingulate cortex (PCC) in order to investigate the associations between PCC activity and emotional, self-relevant processing. The authors presented cartoon stories either depicting moral dilemmas or ordinary situations, which cue a simple yes/no answer. Results revealed that compared to the simple answer condition, all adolescents showed increased PCC activity during reasoning about moral dilemmas as well as during passive viewing of the moral dilemma outcome. The authors suggest that in adolescents, PCC activity during the morally relevant tasks reflects self-directed attention and implicit emotional engagement with moral challenges. Harenski et al. (2012) used a different paradigm and presented moral pictures (unpleasant social scenes with moral violations), nonmoral pictures (unpleasant social scenes without moral content), and neutral pictures (neutral social scenes without moral content) to healthy males between the ages of 13 and 53 years. The participant's task was to indicate the degree of moral violation severity. While viewing the moral picture, older adults (age range 27–53) in contrast to younger adults (age range 19–25) and adolescents (age range 13–18) showed an increase of activity in the bilateral temporoparietal junction (TPJ). In reference to the role of the TPJ in mentalizing, the authors surmise that adolescents, relative to adults, use less mentalizing strategies during moral judgment and that inference about beliefs and intentions may be progressively integrated during development. Furthermore, Harenski et al. found that moral picture viewing induces more activity in the PCC in older and younger adults compared to adolescents. This result contradicts Pujol et al.'s suggestion that PCC activity may be associated with a core aspect of adolescents' moral reasoning:

emotional engagement and self-directed thinking. These inconsistent findings may result from differences in the paradigms—while Pujol et al. investigated moral reasoning, Harenski et al. investigated the appraisal of social scenes with regard to moral violations. Additionally, the two studies investigated slightly different age groups. Whereas Pujol et al. tested adolescents ranging from 14 to 16 years, Harenski et al. investigated an age range between 13 and 18 years. Considering the variety of hormonal, cognitive, and neuronal changes during the few years of adolescence (e.g., Moshman, 2011; Shaw et al., 2008), this age difference might influence processes related to PCC activity. A recent study by Decety et al. (2012) investigated the contribution of emotion and cognition to moral sensitivity in participants aged between 4 and 37 years. They presented dynamic visual stimuli depicting moral and nonmoral transgressions. After scanning, participants had to rate different questions concerning the intentionality of the action as well as morally relevant questions about the empathic concern for the victim, personal distress, understanding of the perpetrator's mental state, and moral evaluation. All participants rated intentional harm as more wrong than accidental harm. These judgments did not vary with age. Additionally, no age effects were found for ratings concerning empathic concern for victims. Nonetheless, with increasing age, subjects reported feeling less upset when viewing objects being damaged and were less willing to punish agents who intentionally damaged objects than those who intentionally harmed people. On the neural level in all participants, the perception of intentional harm was associated with an increased signal change in the amygdala, the periaqueductal gray (PAG), the insula, the ventromedial prefrontal cortex (vmPFC), and the right posterior sulcus temporalis superior (pSTS)/TPJ. In contrast to Harenski et al. (2012), Decety et al. (2012) found no influence of age on activity of the pSTS/TPJ. Nevertheless, age-related changes were observable in some of these areas when participants viewed intentional harm versus accidental harm: the younger the participants, the higher the activity in the PAG, the temporal poles, the amygdala and the right insula and the older the participants, the higher the activity in the vmPFC. Functional connectivity analysis revealed increased functional integration with age between the amygdala and the vmPFC. The authors suggest that their results reflect a gradual change with age of the complex integration between affective and cognitive processes involved in moral reasoning and emphasize that discomfort induced by negative emotions helps to alert to the moral salience of a situation.

The understanding of the moral domain necessitates the coordination of multiple cognitive and affective processes (Casebeer, 2003). Studies that investigated the neural basis of developing moral cognition reflect this complexity in their different focuses. Pujol et al. (2008) asked for the role of emotional engagement in adolescents' reasoning about moral dilemmas. Harenski et al. (2012) and Decety et al. (2012) investigated different aspects of moral sensitivity, with Harenski et al. (2012) focusing on decisions about the severity of moral violations, and Decety et al. (2012) focusing on affective reactions in the face of intentional or accidental harm. Nonetheless, no studies directly investigated decisions on morally relevant behavior. Yet in everyday life we are frequently confronted with situations in which decisions between the fulfillment of moral obligations toward other persons (e.g., helping people who are in distress) clash with personal-oriented hedonistic behavior. For example, after a long work day, we may run to the bus stop to catch the waiting bus home. At the bus stop, we may see an old woman who has stumbled and needs help. Helping the woman, however, would result in missing the bus. In situations like these we have to decide between two alternative behaviors: we can either decide to fulfill our own desire (e.g., running to the bus to catch a ride home), which may result in self-reproach and shame about our egoism, or we can inhibit our personal desire and fulfill a moral obligation (e.g., helping the old woman), thus resulting in personal disadvantages and discomfort (e.g., a boring wait for the next bus). Using such everyday moral conflicts, we showed that in adults decisions concerning moral situations compared to decisions concerning neutral situations increased activity in a widespread neural network including the medial frontal cortex, temporoparietal areas, and the PCC (Sommer, Rothmayr, et al., 2010). Additionally, personal-oriented decisions in contrast to morally guided decisions were associated with higher rankings of uncertainty and unpleasant emotions and induced significantly more activation in the amygdala/parahippocampal complex (Sommer, Rothmayr, et al., 2010).

In the present study, we aimed at investigating the neural correlates of moral decision making in adolescents compared to adults. For this purpose, we slightly changed our original scenarios. Firstly, we designed a series of conflict scenarios that were more related to adolescents' social life. Secondly, we compared morally relevant stories with scenarios describing socially relevant situations. Subjects had to choose between two possibilities: one that was more socially oriented (e.g., to spend time with friends) and one that was more situation-oriented (e.g., to save money). In our former study (Sommer, Rothmayr, et al., 2010), we contrasted moral conflict situations to neutral situations in which two personal desires clashed with each other (e.g., save time versus save money). This contrast does not rule out the possibility that activity in the moral condition is not only associated with moral reasoning but also with processing social information. Therefore, we used socially relevant situations as baseline condition in the present study. Just as in the moral conflict situations, all social scenarios described social interactions. The only difference between the two conditions was that in the social scenarios a decision for one of the two alternatives did not clash with moral rules (examples of the moral and social stories are presented in Table 1).

The participants' task were to indicate how they would decide if they were in the described situation. Additionally, after the experiment in the scanner, subjects had to indicate how they felt with their response and how sure they were about their response. Besides contrasting moral versus social conflicts, we were especially interested in neural processes associated with moral decision making within the moral conflicts. Therefore, we analyzed the moral conflicts in more detail and contrasted personal-oriented hedonic, but legal, versus morally guided choices.

We suggest that in the moral conflict situations, adolescents and adults will choose the morally oriented alternative more often than the personal-oriented one (Sommer, Rothmayr, et al., 2010). But moral considerations may play a more important role for adolescents than for adults. Adolescence is characterized by increases in self-reflection, empathic orientation, and care-oriented reasoning (Decety et al., 2012; Eisenberg et al., 2009; Pujol et al., 2008). Additionally, adolescents begin to integrate internalized values and increased concern for others in their picture of themselves (Smetana & Turiel, 2003; Steinberg, 2005). Therefore, it is possible that in everyday conflict scenarios that demand decisions between a morally oriented and a hedonistic response, adolescents will try to act more congruent with their own moral demands and will show more morally oriented decisions than adults. On the other hand, developmental studies show that hedonistic reasoning, after an initial decrease from childhood to early adolescence, increases in mid- and late adolescence (Eisenberg et al., 2009). For instance, Colby and Kohlberg (1987) observed that moral thinking of some adolescents regress to different types of value relativism, situation ethics, and egoism. Based on these studies, one could presume that adolescents will show more hedonistic than morally oriented responses compared to adults.

In accordance with our former study (Sommer, Rothmayr, et al., 2010), we suggest that everyday moral conflict situations will induce activity particularly in medial frontal areas, including the dorsal ACC, temporoparietal areas, and the PCC. Given that significant structural brain changes in frontal and parietal areas are observable through adolescence (e.g., Gogtay et al., 2004; Shaw et al., 2008; Sowell et al., 2004; Toga et al., 2006), we expect differential activation especially of these brain regions between adolescents and adults.

# METHODS

## Subjects

Sixteen adolescents (mean age 15.0 years, SD = 0.82 years, range = 14–16 years; 7 males) recruited from schools in Regensburg and 16 adults (mean age 24.9 years, SD = 2.96, range = 22–31 years; 8 males) with no history of neurological or psychiatric problems participated in the study. All participants were right-handed. Written informed consent was obtained from all subjects, and all procedures were conducted as approved by the local Ethics Committee.

IQ was assessed with a verbal measure of intelligence (MWT-B; Lehrl, 2005). The mean IQ of the adolescents was 109.5 (*SD* = 9.73) and that of adults was 109.9 (SD = 10.1). The difference was not significant. All subjects reported being raised in Germany and speaking German as their native language. In total, 13 out of the 16 adults and 14 out of the 16 adolescents reported having a Christian background, while the remaining subjects reported no religious background.

## Experimental design

The design was similar to that of Sommer, Rothmayr, et al. (2010). Only the content of the stories were exchanged and adapted to situations more adequate for adolescents. Subjects were presented with a total of 56 stories describing conflicts with either moral or social content. The 28 stories with moral content (*moral conflicts* condition) described conflicts requiring a decision between a personal desire and a conflicting

**TABLE 1**

Examples of conflicts and corresponding response alternatives in the *moral conflicts* and the *social conflicts* condition. English translation of the original German-language version

| *Conflict* | *Response alternatives* |
|---|---|
| *Moral conflicts* | |
| I want to board the subway train that is about to leave and that runs only every 15 minutes. Next to me on the platform is an old man with a bag of groceries. As I am getting on the train, he accidentally drops the bag on the floor.<br>What should I do? | Take the train<br>Help the man |
| On the street I find a wallet with 50€ in it but with no information about its owner. There is no possibility to find out who owns the wallet. However, I could turn in the wallet at the city's lost property office.<br>What should I do? | Turn in the wallet<br>Keep the wallet |
| I am running to catch the bus which only leaves every hour. In front of me a woman with two small children drops several items from her purse. Besides me no one else is around to help the woman. What should I do? | Help the woman<br>Catch the bus |
| At a department store I discover my dream jeans. On the way to the cash register I remember a report on child labor which I have recently seen on TV. The brand name of the clothes I want to buy was mentioned there, too.<br>What should I do? | Not buy the jeans<br>Buy the jeans |
| I am at a club that is really packed tonight. After I finally get my drink I realize that the barkeeper has given me 10€ too much in return. In order to give the money back I would have to get in line again.<br>What should I do? | Keep the money<br>Give the money back |
| I am very tired and I am sitting on the bus home. At the next stop a woman with crutches gets on the bus. All seats in the bus are taken.<br>What should I do? | Offer my seat<br>Stay in my seat |
| The soccer world cup final is on TV tonight. I am a big soccer fan and I am looking forward to the game. All of a sudden a friend who is not feeling well calls and wants to meet up with me.<br>What should I do? | Watch the soccer game<br>Meet up with my friend |
| A friend of mine and I want to buy a brand-new computer game. I promise to get the game at the store for the two of us. However, at the store there is only one game left.<br>What should I do? | Buy the game for myself<br>Buy the game for my friend |
| *Social conflicts* | |
| Together with my friend, who is very interested in fashion, I am at a clothing store looking at a shirt. My friend likes a stylish shirt which costs 60 Euros, but I am broke and favorite a shirt which costs 30 Euros.<br>What should I do? | Buy my friend's favorite for 60 Euros<br>Buy my own favorite for 30 Euros |
| My bicycle is broken. A professional in the bike store would be able to repair the bike immediately for 200 €. A friend who has momentary a lot of work in school would be able to repair the bike for 120 €.<br>What should I do? | Have it repaired by the professional<br>Have it repaired by the friend |
| Together with my friends I watched a DVD from a DVD rental store this evening. If I brought back the DVD to the store tomorrow it would cost me double as much as if I brought it back tonight, but then I must leave my friends.<br>What should I do? | Bring back the DVD tonight<br>Bring back the DVD tomorrow |
| I am on a walk and passing by an ice-cream van in which one of my friends is working. I decide to buy my favorite ice-cream. My friend recommends another kind of ice-cream.<br>What should I do? | Take my favorite ice-cream<br>Take the recom-mended ice-cream |
| I would like to buy a birthday present for a friend. I know my friend wants to have a photo book about his favorite rock band, but the book shop has only a photo book about pop bands in general. The birthday is tomorrow.<br>What should I do? | Buy the book about pop bands<br>Try to get the book in another store |
| I promise to buy a certain kind of gummi bears for a friend who really likes them. The shop owner tells me that all packages of that kind are sold out. He recommends gummi bears of a different brand but I do not know if my friend like them.<br>What should I do? | Buy the other gummi bears<br>Not buy any gummi bears |
| I want to buy flowers for my friend, but the supermarket around the corner doesn't really have a big selection. However, I know of a flower shop that has a bigger selection. In order to get there I would have to drive 15 minutes and it is raining.<br>What should I do? | Buy flowers from the nearby market<br>Drive to the other store |

(*Continued*)

**TABLE 1**
(Continued)

| *Conflict* | *Response alternatives* |
|---|---|
| In order to get to school I can take the slow bus line 1 in which a friend is sitting and the faster bus line 2. At the bus stop the line 1 bus arrives, but is packed with people. Five minutes later a bus from the faster bus line 2 would arrive. What should I do? | Take the packed bus<br>Take the slower bus |

moral standard (e.g., helping people in distress, being honest). The other 28 stories (*social conflicts* condition) subsequently required subjects to choose between a more socially oriented or a more situation-oriented option. All conflict stories, the moral as well as the social, described interactions with other people. Yet only the moral conflict stories demanded morally relevant decisions. The social conflict stories involved no morally relevant aspects and neither the social-oriented nor the situation-oriented judgment caused significant social consequences. Each trial in both conditions started with the presentation of a conflict in text form followed by the question, “How should I decide?”. The conflicts were presented in first-person narrative and remained on the screen for 15 s. Examples of the moral and social conflict stories translated from German into English are presented in Table 1. Stories in both conditions had been matched in terms of reading time and number of words. In a behavioral study with 16 participants, we provided evidence that people are capable of reading the scenarios within this time period and that there are no differences in average reading time between the two conditions (social conflicts: mean reading time 13.62 s (SD = 0.16); moral conflicts: mean reading time 13.76 s (SD = 0.20); t(15) = 1.6, n.s.).

Every conflict trial was followed by the presentation of the two possible response alternatives presented at the center of the screen for 5 s. Responses were also given in first-person narrative. After the presentation of the responses, the letters “A” and “B” were displayed above the left and right response alternative, respectively. Subjects were instructed to indicate their decision with the press of one of two buttons of a response pad with their right middle and index finger as soon as the letters appeared on the screen. This slide appeared on the screen for 2 s. Subjects were instructed to press a button upon the appearance of the letters in order to exclude neural activation attributable to motor processes in the subsequent statistical analysis. Every trial was followed by a fixation period with a fixation cross at the center of the screen with a randomly varying duration between 8 and 12 s. A schematic depiction of a trial is shown in Figure 1.

Moral conflicts and social conflicts were presented in random order. Responses were presented randomly at the two possible locations.

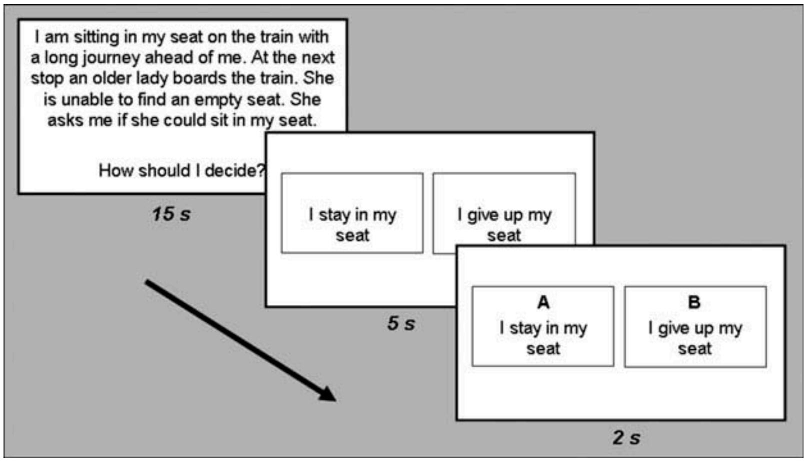


**Figure 1.** Schematic depiction of a trial in the moral conflicts condition. In the first slide, the subjects were instructed to think about what they would do in the conflict presented to them. The two possible response alternatives were then presented, followed by the appearance of the letters “A” and “B.” These letters indicated to the subjects to press a button corresponding to the previously chosen response.

Entire scanning time for functional data acquisition was approximately 30 min. A structural image of the subject's brain was acquired toward the end of the experiment lasting about 7 min.

Prior to the experiment in the scanner, subjects were shown a standardized instruction emphasizing that the subjects should put themselves in the shoes of the protagonist described in the conflict stories. Subjects also participated in a trial experiment on a standard PC outside the scanner consisting of four moral and four social conflicts. None of these conflicts were used in the subsequent fMRI experiment.

The experiment was generated with Presentation 11.3 software (Neurobehavioral Systems Inc., Albany, CA). For the fMRI experiment, stimuli were back-projected onto a mirror inside the scanner. The subjects' responses in the scanner were recorded with an LUMItouch optical response device (Photon Control, Burnaby, Canada).

After the experiment in the scanner, subjects had to fill out a questionnaire containing the 56 social and moral conflicts presented in the scanner. Subjects were required to once again indicate their responses and to also state how sure they were about their decision as well as how good they felt with their decision. Both of these latter questions had to be answered by means of a five-point scale (certainty: 1 = extremely unsure, 5 = extremely sure; emotion rating: 1 = extremely bad, 5 = extremely good).

### *FMRI parameters*

A 3-Tesla Siemens Allegra Head Scanner (Siemens Inc., Erlangen, Germany) located at the University Medical Center Regensburg was used to record the imaging data. The scanner acquired echo-planar-imaging (EPI) sequences using fast gradients. During T2* data acquisition, we recorded 32 slices (whole brain; slice thickness = 3 mm, no skip) in interleaved order with a time-to-repeat (TR) of 2000 ms, a time-to-echo (TE) of 30 ms, a flip angle of 90º, a field of view (FoV) of 192 × 192 mm and a voxel size of 3 × 3 × 3 mm. A total of 964 functional images were recorded in the entire experiment.

A structural image was recorded from every subject at the end of functional data acquisition. These T1-weighted images were obtained using a MPRAGE (magnetization prepared rapid acquisition gradient echo) pulse sequence (TR = 2250 ms, TE = 3.93 ms, flip angle = 9º, FoV = 256 × 256 mm), scanning 160 slices with isotropic voxels of 1 × 1 × 1 mm.

## Data analysis

### *Behavioral data*

Behavioral data acquired during the fMRI experiment as well as in the questionnaire were analyzed statistically with SPSS 16 software (SPSS Corp., Chicago, IL). For the moral conflicts, the number of moral-guided and personal-guided decisions and for the social conflicts the numbers of social-oriented and situation-oriented decisions were analyzed using the nonparametric Wilcoxon test. The certainty about the decision and the emotional reaction during the decision process were analyzed using paired t-tests.

### *Functional imaging data*

All imaging data were analyzed with SPM5 (http://www.fil.ion.ucl.ac.uk/spm/software/spm5) software based on Matlab 7.0 (Math Works Inc., Nattick, MA, USA).

Individual subjects' data were slice-timed, motion-corrected, normalized to a functional template contained in SPM5 (Montreal Neurological Institute template) and smoothed with a Gaussian kernel of a full-width at half maximum (FWHM) of 8 mm.

In the subsequent block design, six individual first-level regressors were modeled. Three separate regressors were modeled in both the *moral conflicts* as well as in the *social conflicts* condition. The first regressor in every condition comprised the entire duration of the conflict presentation (15 s). The second regressor in each condition spanned the presentation time of the response alternatives (5 s). The third regressor focused on the third slide, which showed the letters "A" and "B" above the response alternatives, indicating to subjects to then press a response button (2 s). In addition to the latter regressors, six regressors including movement and translation parameters of the individual subject were also modeled in the design matrix. The hereby created model was then estimated based on the assumptions of the general linear model (GLM). In order to identify brain areas related to moral reasoning, we contrasted the regressor covering the conflict and question presentation in the *moral conflicts* condition to the corresponding regressor in the *social conflicts* condition.

Single-subjects' first-level contrasts were introduced in second-level random-effect analysis to allow for population inference. First, one-sample *t*-tests for all contrasts were conducted separately for adults and adolescents. Second, in order to test the influence of age we investigated the interaction between group (adults and adolescents) and condition (moral conflicts and social conflicts). The resulting set of significant voxel values for each contrast constituted SPM maps that were thresholded at $p < .001$ (uncorrected, 10 or more contiguous voxels). All fMRI results reported here are based on voxel statistics computed with SPM for the entire brain and survived a statistical FWE-corrected cluster threshold of $p < .05$. The activated brain regions were overlaid on the MNI template and labeled according to the Talairach atlas (http://www.bioimagesuite.org/Mni2Tal).

In addition to the analysis that focused on brain regions associated with moral versus social conflicts, we applied a second analysis on the moral conflict condition that attempted to identify brain activity related to choosing a hedonist response versus choosing a morally guided response. For this purpose, we first identified the individual subjects who for moral conflicts had given personal desire-oriented responses at a level of at least 25% of responses (equal to at least 7 out of 28 responses). This was done in order to build additional regressors consisting of a sufficient amount of data points for subsequent analysis. In total, 12 subjects out of the 16 adolescents and 10 subjects out of the 16 adults showed a response pattern of at least 25% personal desire-oriented responses in the conflicts with moral content. The data of these subjects were then introduced into yet another first-level analysis. This analysis included the same regressors as in the original analysis with the only exception of the regressor *moral conflicts*, which was divided into the regressors *immoral decision* (i.e., choosing the subsequent personal desire-oriented response) and *moral decision* (choosing a subsequent morally guided response) based on the subjects' decision in the conflicts of moral content. In order to identify brain regions associated with choosing moral over personal desire-oriented responses, activity in the *immoral decision* condition was subtracted from activity in the *moral decision* condition. Brain activity related to choosing personal or immoral responses over moral responses were revealed by the subtraction of activity in the *moral decision* condition from the *immoral decision* condition. Individual contrast images stemming from first-level analyses were then introduced into a random-effects group analyses. First, main effects for both age groups were analyzed separately. Second, for revealing the influence of age on the neural correlates associated with moral and immoral decisions, interaction effects between age (adults, adolescents) and decision type (moral, immoral) were analyzed. All reported brain regions survived a statistical FWE-corrected cluster level at $p < .05$. The activated brain regions were overlaid on the MNI template and labeled according to the Talairach atlas (http://www.bioimagesuite.org/Mni2Tal).

# RESULTS

## Behavioral results

### *Behavioral results during scanning*

In the *moral conflicts* condition, adolescents chose a morally guided response in an average 60.0% ($SD$ = 18.1%) of the conflicts. Responses fulfilling a conflicting personal desire were on average chosen in 32.8% ($SD$ = 13.6%) of moral conflicts. This difference was statistically significant ($t(15) = 3.76$, $p < .01$). In the *social conflicts* condition, adolescents chose a social-oriented response in 51.9% ($SD$ = 11.4%) and a situation-oriented response in 49.5% ($SD$ = 9.8%) of the social conflicts. In contrast to our hypothesis, this difference was statistically not significant. Adults chose a morally guided response an average of 71.9% of the time ($SD$ = 10.7%) in the *moral conflicts* condition. The fulfilling of a personal desire was chosen an average of 25.7% ($SD$ = 10.4%) of the time for the conflict situations. The difference between the two conditions was significant ($t(15) = 8.85$, $p < .001$). In the *social conflicts* condition, the adults chose 48.7% ($SD$ = 9.4) socially oriented and in 50.4% (SD = 11.8) situational-oriented. The difference was statistically not significant. The comparison of the two groups revealed for the *moral conflicts* condition that adults gave significantly more morally guided responses than adolescents ($t(30) = 2.24$, $p < .05$). For the *social conflicts* condition, the two groups showed no differences in their judgments.

For adolescents, mean reaction time (RT) when choosing the morally guided response in the *moral conflicts* condition was 705 ms ($SD$ = 191 ms). Mean RT when choosing the personal desire conflicting with a moral standard was 785 ms ($SD$ = 255 ms). A paired $t$-test revealed that this difference was statistically not significant ($t(15) = 1.9$; n.s.). Mean RT in the *moral conflicts* condition amounted to 745 ms ($SD$ = 209 ms). In the *social conflicts* condition, there was no difference between social-oriented (729 ms, $SD$ = 201 ms) and situation-oriented (741 ms, $SD$ = 189 ms) decisions. Mean RT in *social conflicts* amounted to 735 ms ($SD$ = 247 ms). No statistically significant difference was revealed between RT in the *moral conflicts* and the *social conflicts* condition ($t(15) = .336$; n.s.). For adults in the *moral conflicts* condition, mean RT when choosing the morally guided response was 809 ms (*SD* = 291 ms). Mean RT when choosing a personal desire was 876 ms (*SD* = 272 ms). A paired *t*-test revealed no significant differences between the two conditions ($t(15) = 1.4$; n. s.). In the *social conflicts* condition, mean RT for the social-oriented (797 ms, *SD* = 212 ms) and the situation-oriented decisions (803 ms, *SD* = 246 ms) did not significantly differ. Adults and adolescents showed no significant differences in their RT, neither in the *moral conflicts* condition (morally guided responses: $t(30) = 1.19$, n.s., personal-guided responses: $t(30) = 1.67$, n.s.) nor in the *social conflicts* condition (social-oriented responses: $t(30) = 1.43$, n.s., situation-oriented responses: $t(30) = 1.57$, n.s.).

### *Behavioral results of the postscanning questionnaire*

The analyses of the postscanning behavioral data confirmed the subjects' response pattern observed in the fMRI scanner. Adolescents chose a morally guided response an average of 62.26% (*SD* = 17.3%) of the time and a personal desire-guided response an average of 36.6% (*SD* = 16.3%) of the time for *moral conflicts*. This difference was statistically significant ($t(15) = 3.06$, $p < .01$). In the *social conflicts* condition, adolescents chose a socially oriented response in 52.6% (SD = 11.9%) and a situation-oriented response in 47.1% (*SD* = 10.4%) of the conflicts. This difference was statistically not significant.

Adults chose a morally guided response an average of 73.6% (*SD* = 11.2%) and a personal desire-guided response an average of 26.3% (*SD* = 11.2%) of the time for the *moral conflicts* condition. The difference between the two conditions was significant ($t(15) = 8.44$, $p < .001$). In the *social conflicts* condition, the adults chose 49.5% (*SD* = 9.9) socially oriented and 48.7% (*SD* = 12.8) situational-oriented responses. The difference was statistically not significant.

For the *moral conflicts* condition, the comparison of the two groups revealed that adults gave significantly more morally guided responses than adolescents ($t(30) = 2.21$, $p < .05$). There were no group differences in the *social conflicts* condition.

Adolescents reported significantly more negative emotions in situations in which they decided to act in a personally oriented ($M = 3.0$, $SD = 1.1$) way than in situations in which they decided to act in a morally guided ($M = 4.2$, $SD = 0.6$; $t(15) = 5.5$, $p < .01$), socially oriented ($M = 4.2$, $SD = 0.5$; $t(15) = 5.2$, $p < .001$), or situation-oriented ($M = 4.0$, $SD = 0.7$) manner. Emotion ratings of the morally guided judgments did not differ from judgments in social situations ($t(15) = 1.6$, n.s.). Concerning the certainty of the decisions, adolescents reported no differences between morally guided ($M = 4.1$, $SD = 0.5$), personal desire-guided ($M = 4.0$, $SD = 0.7$), socially oriented ($M = 3.9$, $SD = 0.47$), or situation-oriented ($M = 4.3$, $SD = 0.47$) responses.

Like adolescents, adults also reported significantly more negative emotions during personal desire-guided ($M = 2.3$, $SD = 0.7$) judgments than during morally guided judgments ($M = 4.2$, $SD = 0.5$; $t(15) = 10.1$, $p < .001$), socially oriented ($M = 4.0$, $SD = 0.6$), or situation-oriented judgments ($M = 3.9$, $SD = 0.5$). But in contrast to adolescents, they indicated lower certainty associated with personally oriented decisions ($M = 3.4$, $SD = 0.7$) in contrast to morally guided ($M = 4.3$, $SD = 0.4$; $t(15) = 4.0$, $p < .001$), social-oriented ($M = 4.1$, $SD = 0.5$, $t(15) = 3.8$, $p < .01$) or situation-oriented decisions ($M = 4.2$, $SD = 0.5$, $t(15) = 3.9$, $p < .01$).

The direct comparison between the two groups revealed that in the social situations, adolescents and adults did not differ in their emotion ($t(30) = 0.4$, n.s.) and certainty ratings ($t(30) = 0.5$). In morally relevant situations, there were also no differences between the two age groups in the emotion ratings ($t(30) = 1.7$, n.s.), but adults were significantly less certain than adolescents in moral conflict situations in which they had to decide for a personal-guided behavior ($t(30) = 2.26$, $p < .05$).

## Functional imaging results

In order to reveal regions in the brain dedicated to everyday moral reasoning, we subtracted activity during conflict and question presentation (duration: 15 s) in the *social conflicts* condition from the corresponding activity in the *moral conflicts* condition to single out the crucial process of moral reasoning.

For the adults, significant activation in the comparison *moral conflicts* > *social conflicts* was revealed in a broad cluster of the medial prefrontal cortex (BA 8, 9, 10), the bilateral TPJ/inferior parietal gyrus (BA 39, 40), the bilateral insula extending to the inferior frontal gyrus (BA 13, 45, 47), and the bilateral PCC/precuneus (BA 31, 7). Adolescents showed increased activity associated with *moral conflicts* in contrast to *social conflicts* in a broad cluster of the medial frontal cortex (BA 6, 8, 9, 10), the right inferior frontal gyrus extending to the middle temporal gyrus (BA 47, 21), the left inferior frontal gyrus (BA 45, 47), the bilateral TPJ/inferior parietal cortex (BA 39, 40), the right thalamus, the left parahippocampal gyrus, the left

**TABLE 2**
Analysis of brain activity associated with *moral conflicts* in contrast to *social conflicts*: main effects of group and interaction between group and task. The results were FWE-corrected at the cluster level ($p$ < .05)

| *Brain region* | *Center MNI coordinates*[a] | | | *Z-score* | *Cluster size in voxels*[b] |
|---|---|---|---|---|---|
| | *x* | *y* | *z* | | |
| *Adults* | | | | | |
| Medial frontal cortex (BA 8/9/10) | 6 | 52 | 26 | 7.96 | 9324 |
| Right temporoparietal junction/ inferior parietal lobe (BA 39/40) | 56 | −54 | 28 | 6.90 | 3592 |
| Left temporoparietal junction/ inferior parietal lobe (BA 39/40) | −54 | −52 | 22 | 5.89 | 1932 |
| Right insula/inferior frontal cortex (BA 13/45) | 32 | 20 | −12 | 6.17 | 1542 |
| Left insula/inferior frontal cortex (BA 13/47) | −30 | 20 | −10 | 5.56 | 570 |
| Bilateral posterior cingulate cortex/ precuneus (BA 31/7) | 4 | −58 | 42 | 6.65 | 4617 |
| *Adolescents* | | | | | |
| Medial frontal cortex (BA 8/9/10) | 8 | 56 | 24 | 6.45 | 4476 |
| Right middle frontal cortex (BA 6) | 14 | 20 | 64 | 5.31 | 378 |
| Right inferior frontal gyrus/middle temporal gyrus (BA 47/21) | 54 | −2 | −22 | 5.39 | 2518 |
| Left inferior frontal gyrus (BA 47/45) | −30 | 20 | −12 | 4.66 | 367 |
| Right temporoparietal junction/ inferior parietal lobe (BA 39/40) | 56 | −52 | 32 | 5.45 | 1776 |
| Left temporoparietal junction/ inferior parietal lobe (BA 39/40) | −52 | −54 | 20 | 5.47 | 1951 |
| Right thalamus | 14 | −30 | 6 | 5.06 | 462 |
| Left parahippocampal gyrus (BA 37) | −34 | −38 | −12 | 5.03 | 326 |
| Left hippocampus | −36 | −10 | −14 | 4.42 | 636 |
| Bilateral posterior cingulate cortex/ precuneus (BA 31/7) | 2 | −60 | 54 | 6.07 | 4435 |
| *Group × task interaction* | | | | | |
| Left parahippocampal region (BA28) | −16 | −12 | −14 | 3.82 | 52 |

*Notes*: [a]Coordinates refer to the Montreal Neurological Institute (MNI) reference brain. Brodmann areas (BA) are approximate. [b]Voxel sizes amounted to 2 mm × 2 mm × 2 mm.

hippocampus, and the bilateral posterior cingulate/precuneus (BA 31, 7). For both groups, a detailed description of significant activity in the contrast *moral conflicts* > *social conflicts* is shown in Table 2, while Figure 2 shows an overly of the activity of the adolescents and adults in the contrast *moral conflicts* > *social conflicts.*

The main focus of the current study has been the influence of age on the neural correlates associated with morally relevant everyday decisions. A significant interaction between the two age groups (*adolescents, adults*) and the two conditions (*social conflicts, moral conflicts*) was found in the left parahippocampal region ($x = -16$, $y = -12$, $z = -14$; $F(1,60) = 18.34$; cluster size = 52). Post hoc $t$-tests revealed that in the parahippocampal region, adolescents showed a significant activity increase during morally relevant decisions compared to decisions in social situations ($t(30) = 3.55$, $p < .01$). Adults showed the reverse effect with significantly less activity during moral conflict processing and more activity during social conflict processing ($t(30) = -2.4$, $p < .05$). The parameter estimations for this interaction are depicted in Figure 3.

To further analyze the brain activity of adolescents during the processing of moral conflicts, we exclusively masked the contrast *moral conflicts* > *social conflicts* in adolescents with the same contrast in adults at $p = .05$. Results revealed that adolescents, in contrast to adults, showed activity in the left lateral anterior rostral prefrontal cortex, the left inferior frontal cortex, the right middle temporal gyrus, the left parahippocampal area, and the right thalamus during moral decision making (Table 3).

In addition to the analysis of brain regions associated with moral versus social conflicts, we investigated the moral conflicts in more detail and applied a second analysis on the moral conflict condition. This analysis attempted to identify brain activity in adolescents and adults related to choosing a hedonistic response versus choosing a morally guided response. In total, 12 of the 16 studied adolescents and 10 of the 16 studied adults showed a response pattern of at least 25% morally guided/personal desire-oriented decisions in the moral conflict condition.

In adults, morally guided decisions in contrast to personal desire-guided decisions induced more activation only in the right anterior cingulate cortex.

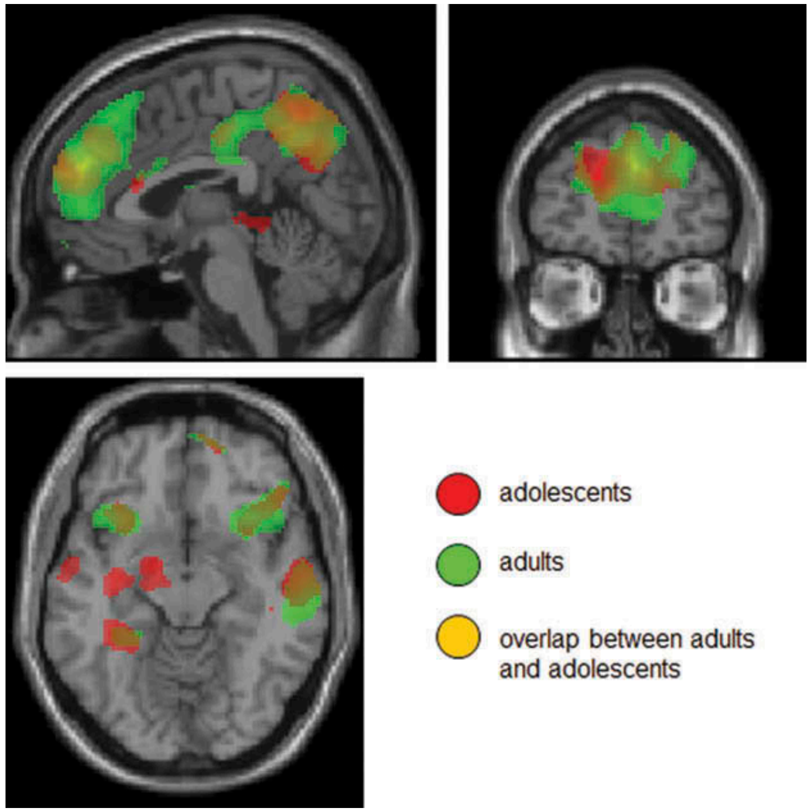


**Figure 2.** Overlay of the significant activity of the adolescents (red) and adults (green) in the contrast *moral conflicts* > *neutral conflicts*. Overlap of the activation of both groups is shown in yellow. Clusters with significant activity at a FWE-corrected $p$-value of $\leq .05$ on cluster level are shown on template views of the brain. Activity is depicted on a medial view of the brain at MNI coordinates $x = 0$, a coronal view at $y = 50$ and a horizontal view at $z = -12$ (clockwise, from top left).

Adolescents showed activity associated with morally guided responses in contrast to personal desire-guided responses in the medial frontal gyrus, the anterior cingulate cortex, the right superior frontal gyrus, the left TPJ/inferior parietal lobe, and the PCC/precuneus. A detailed description of significant activity in the contrast morally guided > personal desire-oriented for both groups is shown in Table 4. The reverse contrast (personal desire-oriented > morally guided) showed no significant activations for neither the adults nor the adolescents. The significant interaction effects between group and decision type revealed increased activity for adolescents associated with morally guided responses in contrast to personally oriented responses in the anterior cingulate cortex, the right dorsolateral prefrontal cortex, the left inferior parietal cortex/TPJ, and the left and right PCC.

Exclusively masking adolescents (morally guided > personal desire-oriented) with adults (morally guided > personal desire-oriented) indicated that adolescents showed activity only in the medial frontal cortex, the anterior cingulate cortex, the right middle temporal gyrus, the left TPJ/inferior parietal cortex, and the PCC (for a detailed description of the results, see Table 5 and Figure 4).

## DISCUSSION

The aim of the present study was to investigate developmental cortical changes that are associated with everyday moral reasoning. Specifically we were interested in the question of whether behavioral or neural differences exist between adolescents and adults related to choosing a hedonistic response versus choosing a morally guided response. Therefore, we presented moral and social conflicts to adolescents between 14 and 16 years of age and adults. The moral as well as the social conflicts described social situations and subjects had to decide explicitly between two alternative behavior strategies. In the moral conflict situations, they could decide to follow a moral rule or to fulfill a personal desire. In the social conflict situations they had to decide between socially oriented and situation-oriented alternatives.

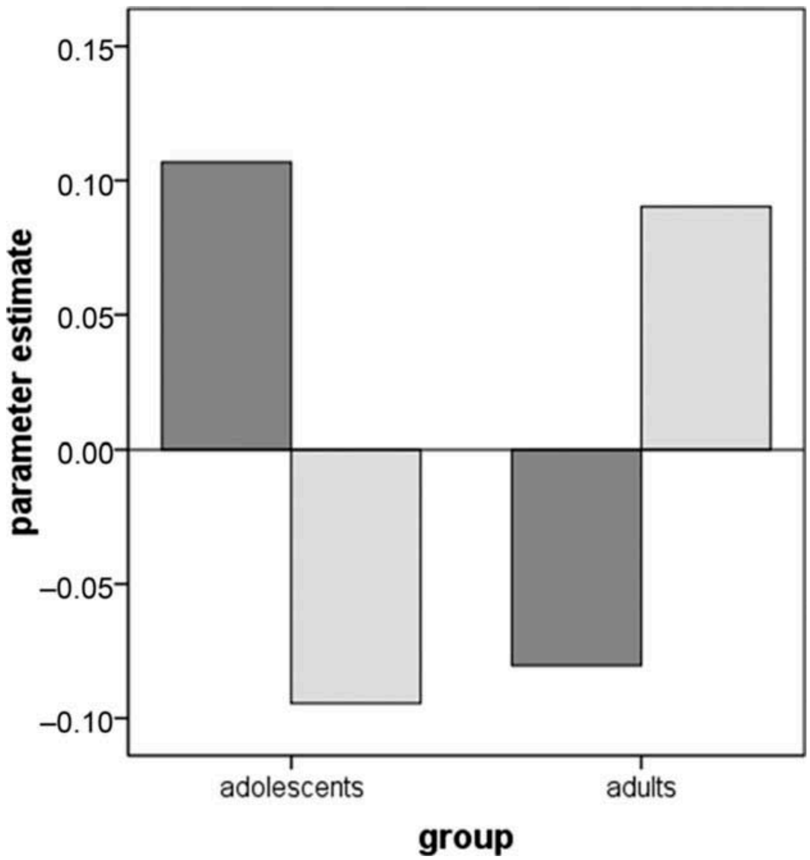


**Figure 3.** Parameter estimations of the left parahippocampal region ($x = -16$, $y = -12$, $z = -14$) for the significant interaction between the two age groups (*adolescents, adults*) and the two conditions (*social conflicts, moral conflicts*). Post hoc *t*-tests revealed that in this region adolescents showed a significant activity increase during morally relevant decisions compared to decisions in social situations. Adults showed the reverse effect with significant less activity during moral conflict processing and more activity during social conflict processing.

**TABLE 3**
Regions of increased brain activity of adolescents revealed by exclusively masking the contrast adolescents (*moral conflicts* > *social conflicts*) by adults (*moral conflicts* > *social conflicts*). The results were FWE-corrected at the cluster level ($p < .05$)

| | *Center MNI coordinates*[a] | | | | |
|---|---|---|---|---|---|
| *Brain region* | *x* | *y* | *z* | *Z-score* | *Cluster size in voxels*[b] |
| Left lateral anterior rostral prefrontal cortex (BA 9/10) | −14 | 46 | 18 | 5.66 | 397 |
| Left inferior frontal cortex (BA 45) | −54 | 20 | 0 | 4.02 | 165 |
| Right middle temporal gyrus (BA 21) | 50 | 6 | −24 | 4.34 | 316 |
| Left parahippocampal gyrus | −36 | −10 | −14 | 4.42 | 575 |
| Right thalamus | 14 | −30 | 6 | 5.06 | 452 |

*Notes*: [a]Coordinates refer to the Montreal Neurological Institute (MNI) reference brain. Brodmann areas (BA) are approximate.
[b]Voxel sizes amounted to 2 mm × 2 mm × 2 mm.

## Behavioral results

The *social conflicts* condition was constructed so that the stories involved social conflict situations in which a more socially oriented (e.g., to spend time with friends) or a more situation-oriented (e.g., to save costs) decision was possible. The behavioral findings showed that neither the adolescents nor the adults preferred one of the two alternatives and that there were no differences in certainty and emotion ratings between the two possible responses. Possibly, the similar distribution of socially and situation-oriented responses in both age groups reflects that the situation-oriented decisions would not cause significant

**TABLE 4**
Analysis of brain activity associated with morally guided decisions in contrast to personal-desire guided decisions: main effects of group and interaction between group and task

| *Brain region* | *Center MNI coordinates*[a] *x* | *y* | *z* | *Z-score* | *Cluster size in voxels*[b] |
|---|---|---|---|---|---|
| *Adults* | | | | | |
| Right anterior cingulate cortex (BA 32) | 24 | 42 | 10 | 3.88 | 438 |
| *Adolescents* | | | | | |
| Medial prefrontal gyrus (BA 8/9/10/) | −8 | 50 | 46 | 4.00 | 3117 |
| Anterior cingulate cortex (BA 32) | 4 | 24 | 34 | 4.10 | 384 |
| Right superior frontal gyrus (BA 8) | 24 | 44 | 48 | 3.80 | 360 |
| Left temporoparietal junction/inferior parietal lobe (BA 39/40) | −44 | −52 | 32 | 4.42 | 1248 |
| Posterior cingulate cortex/precuneus (BA 31/7) | −8 | −22 | 22 | 3.99 | 3209 |
| *Group × task interaction* | | | | | |
| Right dorsolateral prefrontal gyrus (BA 8/9) | 26 | 26 | 54 | 4.38 | 140 |
| Anterior cingulate cortex (BA 24) | −8 | 28 | 16 | 4.06 | 37 |
| Left temporoparietal junction/inferior parietal lobe (BA 39/40) | −40 | −68 | 36 | 3.64 | 22 |
| Right posterior cingulate cortex (BA 31) | 14 | −40 | 30 | 4.47 | 177 |
| Left posterior cingulate cortex (BA 31/24) | −10 | −34 | 34 | 4.10 | 166 |

*Notes*: [a]Coordinates refer to the Montreal Neurological Institute (MNI) reference brain. Brodmann areas (BA) are approximate. [b]Voxel sizes amounted to 2 mm × 2 mm × 2 mm.

**TABLE 5**
Regions of increased brain activity of adolescents revealed by exclusively masking the contrast adolescents (morally oriented > personal desire-oriented) by adults (morally oriented > personal desire-oriented). The results were FWE-corrected at the cluster level ($p < .05$)

| *Brain region* | *Center MNI coordinates*[a] *x* | *y* | *z* | *Z-score* | *Cluster size in voxels*[b] |
|---|---|---|---|---|---|
| Anterior cingulate cortex (BA 32) | 12 | 18 | 26 | 4.11 | 200 |
| Medial prefrontal cortex (BA 10) | −4 | 58 | −4 | 4.21 | 823 |
| Right dorsolateral frontal gyrus (BA 9) | 24 | 28 | 54 | 4.29 | 177 |
| Left dorsolateral prefrontal gyrus (BA 9) | −10 | 51 | 35 | 3.84 | 174 |
| Medial superior prefrontal cortex (BA 6) | 8 | −34 | 74 | 4.19 | 258 |
| Right middle temporal gyrus (BA 21) | 68 | −14 | −20 | 4.30 | 265 |
| Left temporoparietal junction/ inferior parietal lobe (BA 39/40) | −44 | −56 | 34 | 5.74 | 545 |
| Posterior cingulate cortex (BA 31) | −8 | −36 | 36 | 4.78 | 2133 |

*Notes*: [a]Coordinates refer to the Montreal Neurological Institute (MNI) reference brain. Brodmann areas (BA) are approximate. [b]Voxel sizes amounted to 2 mm × 2 mm × 2 mm.

social costs and therefore did not threaten a positive picture of oneself.

In the moral conflict condition, both age groups chose more morally guided responses than personally oriented responses and both groups reported significantly more negative emotions in situations in which they decided to act in a personally oriented way. However, there were some differences between adults and adolescents concerning the number and certainty of hedonistic decisions. Compared to adults, adolescents gave significantly more personally oriented responses. Additionally, when they decided to act in a personally oriented manner, adolescents reported higher certainty ratings than adults.

In order to make sure that there were no systematic mistakes in the construction of the stimulus material (e.g., conflict situations that were unknown by adolescents because they were only relevant for adults), we analyzed whether there were any specific moral conflict situation in which the adolescents showed a higher probability to answer in a personally oriented manner. However, the analysis showed that the

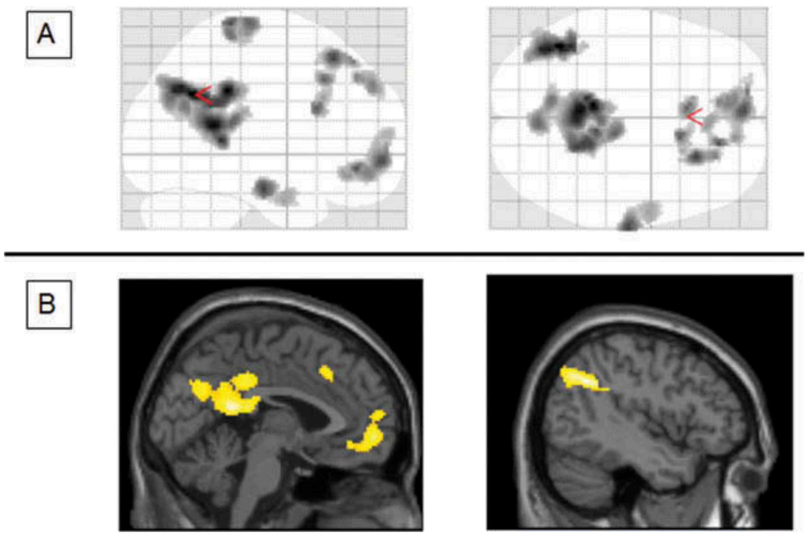


**Figure 4.** Results of the exclusively masking procedure for adolescents' activity in the morally guided > personal desire-oriented contrast (exclusively masked with the contrast adults (morally guided > personal desire-oriented) at $p = .01$). (A) Results are shown on the SPM glass brain. (B) Activity of the adolescents is depicted on a medial view on the MNI template brain (left: $x = -44$; right $x = 0$). Clusters with significant activity at a FWE-corrected $p$-value of $p \leq .05$ on cluster level are shown.

hedonistic responses of the adolescents were evenly distributed over the different morally relevant situations. Therefore, we suggest that the adolescents' higher number of hedonistic responses was not related to systematic mistakes in the construction of our conflict situations.

Another explanation for the response pattern of the adolescents may be that their answers were more impulsive. Yet there are two aspects that seem to contradict this notion. First, adolescents gave more personally oriented responses not only during scanning but also in the postscanning questionnaire, while the completion of this questionnaire was not limited in time. Second, when adolescents decided to act in a personally oriented way, they reported higher certainty ratings than adults but there were no differences in the emotion rating between the two age groups. Adults and adolescents reported significantly more negative emotions associated with personal desire-guided responses than during morally guided responses, indicating that adolescents had reasoned about the consequences of such a behavior and did not only answer impulsively.

Developmental studies revealed great variations in adolescents' pattern of procoscial moral judgments (Eisenberg et al., 2009). Not only self-reflection and the use of internalized values increase in mid- and late adolescence, also hedonistic reasoning (Eisenberg et al., 2009) and value relativism (Colby & Kohlberg, 1987) increase. Our finding that adolescents compared to adults gave more hedonistic responses with higher certainty ratings support developmental studies that revealed an influence of value relativism and self-interest on adolescents' moral reasoning.

Alternatively, the adolescents answered the questions in a more honest way than the adults. Adolescence is characterized as a time period in which people begin to consider their motives, desires, goals, and beliefs and begin to build a theory of themselves (Moshman, 2011). During this time, being authentic is very important and therefore finding higher number of personally oriented decisions in the adolescents may be explained by the personal demand to be honest at this age. Our scenarios described everyday situations in which a moral obligations toward others clash with personally oriented hedonistic needs that would not explicitly cause serious harm to another person. It is possible that adults, who have learned the importance of presenting a socially accepted picture, find it more difficult to admit to personally oriented action tendencies than adolescents, for whom it is more important to present an authentic picture.

## Neural correlates of processing morally relevant situations in adolescents and adults

In adults as well as in adolescents, moral conflicts contrasted with social conflicts induced increased activation in the medial frontal cortex, the bilateral TPJ, the bilateral insula/inferior frontal cortex, and the bilateral PCC. This activity pattern is consistent with the results of a former study of our research group in which we contrasted morally relevant everyday conflict situations with neutral situations in which adult subjects had to choose between two conflicting personal desires (Rothmayr et al., 2011).

In the present study, activity in the medial frontal cortex was associated with the processing of moral compared to social conflicts in both age groups. The important role of the mPFC for moral reasoning throughout the lifespan is supported by lesion and neuroimaging studies. Lesion studies showed that early damage of the mPFC significantly influences the typical maturational trajectory of moral cognition and that late damage of the region led to an impairment in moral reasoning and morally guided behavior (Anderson, Bechara, Damasio, Tranel, & Damasio, 1999; Eslinger, Flaherty-Craig, & Benton, 2004; Eslinger, Grattan, Damasio, & Damasio, 1992; Fumagalli & Priori, 2012; Koenigs et al., 2007; Thomas, Croft, & Tranel, 2011). Also, neuroimaging studies with adults that investigated moral dilemmas compared to nonmoral judgments (Greene et al., 2001; Moll, de Oliveira-Souza, Bramati, & Grafman, 2002) or semantic decisions about the moral or nonmoral content of sentences (Heekeren, Wartenburger, Schmidt, Schwintowski, & Villringer, 2003; Moll, de Oiviera-Souza, Bramati, et al., 2002) found increased activation of the mPFC. Further, a developmental study indicates that activity of the mPFC was also centrally involved in making moral judgments in children and adolescents between 10 and 17 years of age (Eslinger et al., 2009). It is suggested that the mPFC is involved in the integration of social information over time by storing this information in traits or scripts (Van Overwalle, 2009; Van Overwalle, Van Den Eede, Baetens, & Vandekerckhove, 2009). The activity increase of the mPFC in the moral condition may indicate the relevance of scripts for the processing of morally relevant everyday social conflict situations. An alternative, but not incompatible, view is that the activity in this brain region represents the motivational relevance of the social behavior (Moll et al., 2005). In everyday life, moral situations may have a special relevance since for most people acting in terms of morally accepted norms is an important aspect of their self-concept.

In addition to inducing activity in the mPFC, reasoning about everyday moral conflicts produced increased activity in the bilateral TPJ extending into the inferior parietal region. There is a growing body of evidence that the TPJ is centrally involved in the ability to attribute mental states to other people, a process that is known as ToM or mentalizing (Carrington & Bailey, 2009; Döhnel et al., 2012; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004; Schuwerk et al., 2013; Sommer et al., 2007; Van Overwalle, 2009). The ability to understand another person's action in relation of his or her intentions, desires, and beliefs also plays an important role in moral decision making. For example, wrong intentional actions are judged to be worse than similar unintended actions (Lagnado & Channon, 2008) and, depending on the outcome of an action, moral judgments are influenced by a protagonist's neutral or false belief (Young, Cushman, Hauser, & Saxe, 2007).

The results of the present study revealed the involvement of the TPJ in everyday moral decision making and support not only behavioral data that show a strong relationship between progress in moral reasoning and the developing understanding of other peoples' mental states (Killen et al., 2011), but also neuroimaging studies investigating the role of belief attribution on moral judgments (Young, Camprodon, Hauser, Pascual-Leone, & Saxe, 2010; Young et al., 2007; Young & Saxe, 2008, 2009). These studies consistently showed the recruitment of the TPJ during the processing of morally relevant facts (Young & Saxe, 2009) and during the processing of mental states relevant for moral judgments (Koster-Hale, Saxe, Dungan, & Young, 2013; Young & Saxe, 2009, 2008). Moreover, the disruption of the right TPJ by transcranial magnetic stimulation (TMS) led the participants' moral judgments to be less influenced by the actor's mental state and attempted abuses were judged as more permissible (Young et al., 2010).

In both age groups, increased activation associated with the processing of moral conflicts was also found in the PCC and the precuneus. Both areas seem to play an important role in the integration of autobiographical memories and their integration with current emotional states (Cavanna & Trimble, 2006; Fink et al., 1996) and in decision-making processes (Torta & Cauda, 2011). It might therefore be cautiously concluded that moral judgments refer to past experiences. Especially in situations in which a personal desire conflicts with a moral standard, it might be helpful to consider past experiences with emotional consequences of a certain behavior. This may be helpful to guide future decisions in morally relevant situations (Moll et al., 2005). In contrast, for situations in which there are no serious disadvantages for oneself or others, decisions may be less influenced by emotions.

The meaning of memory processes for everyday moral judgments is supported by the significant interaction effect between age groups and condition on parahippocampal activation. For adolescents, increased activity was found during processing of moral, in contrast to social scenarios. Adults showed the reverse effect (see also Figure 3). Several studies reported that activity in the parahippocampal cortex is associated with recollection and may be involved in the processing of contextual associations (Eichenbaum, Lipton, Hasselmo, Moser, & Moser, 2008; Eichenbaum, Yonelinas, & Ranganath, 2007). Possibly, adolescents' increased activity in the parahippocampal region reflects that adolescents refer to past situations for evaluating the morally relevant context more than adults. Due to more social exchanges, adults might have more experience than adolescents with moral situations resulting in heuristics for behavior. In contrast to the moral scenarios that described age-independent general moral conflict situations, the social scenarios described situations that were more related to the life of adolescents. Therefore, adults' increased parahippocampal activity during processing everyday social situations may reflect their reliance on memory for evaluating social contexts that they know better from earlier in life.

In sum, during reasoning about everyday moral conflict situations, adolescents and adults show activity increase in the mPFC, the bilateral TPJ, and the PCC/precuneus. These areas are not only consistently found in studies investigating moral cognition (Bzdok et al., 2012; Casebeer, 2003; Fumagalli & Priori, 2012; Greene & Haidt, 2002; Moll et al., 2005), but also in studies investigating ToM, the ability to attribute mental states to oneself and others (Carrington & Bailey, 2009; Mar, 2011; Van Overwalle, 2009). These results support assumptions that the neural network underlying moral reasoning is domain-global and represent a common network involved in social cognition (Bzdok et al., 2012; Casebeer, 2003; Fumagalli & Priori, 2012; Greene & Haidt, 2002).

## The influence of age on the neural correlates of moral judgments in everyday conflict situations

Whereas adults showed increased activity associated with morally guided decisions compared to personal-oriented decisions only in the right anterior cingulate cortex (ACC), adolescents showed increased activity in the medial frontal cortex, the ACC, the left TPJ, and the PCC. Additionally, the direct contrast between adults and adolescents by using exclusive masking revealed that in adolescents, morally guided decisions compared with personally oriented decisions were associated with an activity increase in the ACC, the mPFC, the dorsolateral prefrontal cortex (DLPFC), the right middle temporal gyrus (MTG), the left TPJ, and the PCC.

Age-associated effects in these areas were also found in the few studies that investigated neurodevelopmental changes in moral reasoning. Despite the use of different tasks, all of these studies revealed changes in the neural activity associated with age, especially pronounced in the mPFC (Decety et al., 2012), the PCC (Harenski et al., 2012; Pujol et al., 2008), and the pSTS/TPJ (Decety et al., 2012; Harenski et al., 2012), but also in the insula and the amygdala (Decety et al., 2012).

Activity in these areas was also found in many studies investigating ToM (Abu-Akel & Shamay-Tsoory, 2011; Van Overwalle, 2009). An association of moral development with ToM development is supported by research in developmental psychology. For instance, Dunn et al. (2000) have shown that children's understanding of beliefs and emotions is positively correlated with explanations of why a moral transgression against a friend was or was not permissible. Children who justified their views about transgressions in terms of feelings and psychological issues were more advanced in their understanding of beliefs and emotions than children who referred to external punishment or social rules (Baird & Astington, 2004). And recently, by using a large-scale activation likelihood estimation (ALE), a meta-analysis on morality, theory of mind, and empathy could show that moral reasoning recruits areas that are also involved in inferring beliefs and intentions (ToM) and in inferring emotional states (empathy). However, it seems that the neural correlates of moral judgments are much closer to the neural correlates of ToM than to those of empathy (Bzdok et al., 2012). The authors suggest that TPJ, mPFC, and MTG represent potential nodes of a network common to different aspects of social cognition such as morality, ToM, and empathy (Bzdok et al., 2012; Casebeer, 2003; Decety, Michalska, & Akitsuki, 2008; Decety et al., 2012; Decety & Porges, 2011; Fumagalli & Priori, 2012; Greene & Haidt, 2002).

The current study revealed that in adolescents the nodes of the ToM network were particularly active during moral decision making when they chose morally guided responses. Our finding supports and extends the results of neurodevelopmental studies on moral by showing that in adolescents activity in areas associated with ToM is not only associated with moral reasoning but also plays a central role in morally oriented behavior. Smetana and Turiel (2003) proposed that the moral development of adolescents must be seen in context of their developing social knowledge and that their systematic attempts to coordinate moral conceptions with social understanding. The activity of the ToM-associated network during morally oriented decisions may reflect the importance and involvement of social knowledge in adolescents' morally relevant decisions. In the context of a conflict between morally oriented and hedonistic decisions, it may be presumed that adolescents' reasoning about other people's intentions, desires, and emotions governs their morally oriented decisions. In contrast, in adults moral decision making may be more rule-oriented codified through habitual use.

Taken together, the present study showed behavioral and neural differences between adolescents and adults during reasoning about morally relevant everyday situations. Compared to adults, adolescents chose the personally oriented alternative significantly more often than the morally oriented alternative. Further, when they decided to act hedonistically, adolescents reported higher certainty ratings than adults. This response pattern might reflect moral reasoning influenced by value relativism and situation ethics or the adolescents' tendency to be honest and authentic (Moshman, 2011; Smetana & Turiel, 2003). Moreover, morally oriented decisions compared to personal-oriented decisions induced higher activity for adolescents in brain areas that are also centrally involved in ToM, thereby strengthened hypothesis concerning the strong relationship between moral development and the development of ToM abilities (Decety et al., 2012; Dunn et al., 2000).

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