A functional brain imaging study on the neural correlates of altruism in social decision-making

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Abstract

An fMRI study was conducted to explore the neural basis of altruism in social decision-making. The participants were confronted with a non-monetary version of the Prisoner's Dilemma which is one of the earliest games developed in game theory. They could make a choice between that which would lead to their own benefit, but to the harm of another person, and one which denies one's own benefit but would be in the interest of the other person. A comparison between these social problems and a set of matched non-social problems (in which no other person was involved) revealed that a complex neural network of cortical and sub-cortical brain areas is involved in making altruistic or selfish decisions. The findings indicate that the decision to behave altruistically relies on the interactions between cognitive control processes in prefrontal cortex and emotional control processes in the amygdala.

Keywords: social cognition; social neuroscience; altruism; egoism; prisoner's dilemma

Introduction

The present study is part of recent endeavors to understand the neural correlates of social cognition. The general conjecture of this line of research is that humans have developed neural mechanisms for social cognition that produce appropriate responses in social interaction with other people. As part of this research area, important work on the neural correlates of social cognition has been done, for instance, in the fields of social cooperation, moral decision-making, the ability to understand the thoughts and feelings of other people (an ability usually referred to as "theory of mind"), and the differences in neural activity during social mentalizing in the first-person and from the third-person perspective. For all these research areas many good review articles are available (social cognition in general: Adolphs, 2001, 2003; Amodio & Frith, 2006; moral reasoning: Greene & Haidt, 2002; Moll, Zahn, de Oliveira-Souza, Krueger, & Grafman, 2005; theory of mind: Frith & Frith, 1999; Leslie, Friedman, & German, 2004; first-person vs. third-person perspective in social mentalizing: Vogeley & Fink, 2003).

With the present work we want to contribute a new aspect to the field of social cognitive neuroscience. We report an fMRI study that compared decisions on a set of social problems with non-social problems. In the social problems, the participants were faced with a decision to make an egoistic choice (which would lead to their own benefit, but to the harm of another person) or an altruistic choice (which denies their own benefit but would be in the interest of the other person). In the non-social problems, the participants were requested to make choices in which no other person was involved. The social problems resembled the Prisoner's Dilemma game, which is the most widely used paradigm in behavioral sciences to study the roots of cooperation and conflicts between individuals and social groups (Axelrod, 1984). In a Prisoner's Dilemma, an individual can choose between two strategies, either to "cooperate" with another person or to "defect". Each person gains when both cooperate. If only one of them cooperates, the defector gains more. If both defect, both gain very little but not as much as the "cheated" cooperator whose cooperation is not reciprocated.

Development of relatively realistic social dilemmas – A Pilot study

We started with a pilot study to finds a set of relatively realistic social dilemmas. This study was conducted in a class room prior to the brain imaging study. We constructed a pool of 45 narrative episodes which contained social problems and 45 related episodes of analogous topics but addressing non-social problems. Subjects could either respond in an egoistic or in an altruistic manner to the social problems. The social problems described a profound conflict of interest between the protagonist and another person. The participants could either make a choice which will be to their own interests, but at the cost of harm to the other person. Or they could sacrifice their own benefit in favor of the other persons' interest. Here is an example of a social problem:
You are on a diving tour with another person. You have an accident under water. The other's air tank is broken, and you are both jammed in the rocks. The dilemma is that the air of the remaining air tank might be enough for one person to survive until help will arrive, but not for both. If you

keep the entire air for yourself, you have a 50% chance to survive, but the other person has only a 5% chance of survival. If you share the air, you both have a 20% chance to survive. If you both try to keep the air for yourself, it comes to a fight, and the chances for both of you are only 10%.

The absolute numbers for wins and losses varied to avoid learning and transfer effects from one task to the other. We also varied how the chances were expressed by partly using absolute values and partly percentages. However, the "qualitative" payoffs were the same in all problems. These relative payoffs are presented in Table 1. The participants could win much if they make an egoistic decision but only if the other (fictive) person would make an altruistic choice. They also could profit, albeit to a lesser extent, if both are altruistic because they get the reward for mutual cooperation. They could lose if both are egoistic but they could lose more if they made an altruistic decision which was not reciprocated by the other person (see Table 1).

		Fictive person	
		Altruistic	egoistic
Protagonist (participant)	altruistic	Win	lose much
	egoistic	win much	lose

Table 1: Payoff matrix

The structure of the non-social problems was very similar to social problems. The only difference was that the participants here were requested to make choices in which no other person was involved. Here is the non-social version of the preceding example:

You are on a diving tour and have an accident under water. The air tank is broken, and you are jammed in the rocks. The dilemma is that the air of your air tank might be not enough to survive until help will arrive. If you stay quiet you save air, but the chance that it is enough until help will come is 50%. If you try to breathe flat you might have a 70% to survive until help will come, but there is also a 30% risk that you become unconscious. If you try to release yourself you might be able to reach the water surface, but you use up much more air, and thus there is a 20% risk that your air tank will be empty by the time you reach the water surface.

Thirty undergraduate students from the University of Oldenburg were tested in two separate sessions with a paper-and-pencil procedure in a classroom. A seven-point scale was used for each problem, ranging from "definitely egoistic" to "definitely altruistic". However, the poles were not labelled with these phrases, but rather with phrases directly related to the problem. From the whole pool of 45 episodes we determined a set of 15 episodes in which we could expect participants to make altruistic decisions and a set of 15 dilemmas in which they most likely will decide egoistically. We excluded 15 social episodes with average ratings. For the selection of the non-social episodes we chose the 15 problems that were rated closest to the mean rating.

Results

Table 2 summarizes the characteristics of the episodes that were selected for scanning. As can be seen in the Table, the group of episodes that were selected as most likely to result in altruistic decisions differed significantly from the group that should result in egoistic decisions. The difference between the groups was statistically significant (Wilcoxon-Test, $Z = 4.98$; $p < 0001$). In the non-social problems we selected the 15 problems that were closest to the mean average rating (Min = 2.2, Max = 6.6; M 4.45; SD 1.16).

	Min	Max	*M*	*SD*
Altruistic	1.5	2.3	2.0	0.67
Egoistic	3.2	4.6	3.7	0.71
All	1.5	4.6	2.9	0.60

Table 2: Results of the norming study.

The neural correlates of altruism in social decision-making – The Imaging study

We tested six male and six female participants. Data from two of the women had to be excluded (due to uncorrectable head movements) from further analyses. The remaining four female and six male participants were all right-handed German native speakers between 19 and 28 years with normal or corrected to normal vision, normal hearing, and no neurological disturbances (mean age 23.7 years, SD 3.09).

Prior to the experiment, the participants were given instructions. Then they were placed in the scanner. The 30 dilemmas and 15 non-social episodes were presented in three runs, each of them consisting of 10 dilemmas and 5 non-social episodes which were randomly selected from the pool and presented in a random sequence. The presentation was implemented as text through a series of three visual displays. The first display posed the scenario, the second introduced the dilemma, and the third posed a question. From the scenario on the first display it was not clear which sort of dilemma (social or non-social) would appear on that trial. In the question, participants were asked what they would do in this situation, for instance, if they would share the air or not. The three displays were presented for a fixed duration of 12, 27, and 9 seconds, respectively, plus a 12 sec inter-trial interval (making a total of exactly 1 minute). During the third display the participants had to press one of two keys for YES (e.g. "share") or No (e.g. "don't share") at their own pace and their responses were recorded. Given that the participants made their choice early within the decision-making period (M = 2912 ms, SD = 1392 ms, including reading times), it seems likely that the 27 seconds period during which the dilemmas were presented on the display involved the main part of the decision making process. For this reason all analyses of hemodynamic responses are based on this second epoch (for the methods of Data acquisition and analysis see the "Appendix").

Results

Table 3 summarizes the behavioral data collected during scanning. Overall, the participants generated more altruistic decisions than egoistic decisions (Wilcoxon-Test: Z = -2.809; p < 0.01). Moreover, although subjects were allowed to respond at their own pace, the non-social decisions took more time than the social decisions. The differences in the response times are statistically significant (mean of the altruistic and egoistic versus individual response time t-Test: t = -2.512; p < 0.05), while the separate differences in response times nearly reach the 5% level of significance (altruistic versus non-social, t-Test: t = -2.115; p = 0.064; and egoistic versus non-social, t-Test: t = 2.216; p = 0.054).

	M (%)	*SD* (%)	*M* (RT in ms)	*SD* (RT in ms)
Altruistic social choices	70	7.2	2948	574
Egoistic social choices	29	6.9	2965	646
Non-social choices	99	2.8	3240	637

Table 3: Mean percent and standard deviation of the chosen alternative altruistic or egoistic social choices and the non-social choices during scanning.

The differences in neural activity are presented in Figure 1. All activations were significant at the cluster level calculated with SPM2 (threshold $p = 0.001$; $p \leq 0.05$, corrected).

Panel A) illustrates the activated brain clusters in the *comparison between social choices and non-social choices*. Significant variations in the levels of activation were found in three different cortical regions. The first included areas located in the orbito-frontal cortex (OFC), corresponding to BA 11. The second was situated in the right dorsolateral prefrontal cortex (DLPFC, BA 46 and BA 46/9). The third included large areas of the left and right posterior parietal cortex (PPC) corresponding to the precuneus and the superior and inferior parietal lobule (BA 7, 40). All these areas were more active during social problem processing than during the processing of non-social problems.

Panel B) shows brain areas related to *altruistic social choices versus non-social choices.* Here portions of the OFC (BA 10, 11), the DLPFC (BA 46), and in the PPC (BA 7, 40) were more active during altruistic decisions.

Panel C) shows the activity related to *egoistic social-choices versus non-social choices.* This comparison also resulted in differences in areas in the PPC, but there was no significant increase of activity in the OFC and DLPFC.

Panel D) shows *the direct comparison between altruistic and egoistic choices.* Only the PPC cluster reached the significant level (threshold $t = 4.3$, corrected). However, there is a cluster in the DLPFC under a slightly liberal threshold ($t = 4.0$, $p = 0.002$, uncorrected) No cluster could be found in the opposite contrast (egoistic versus altruistic social choices). Details can be found in Knauff, Fangmeier, Raabe, and Greenlee (2009).

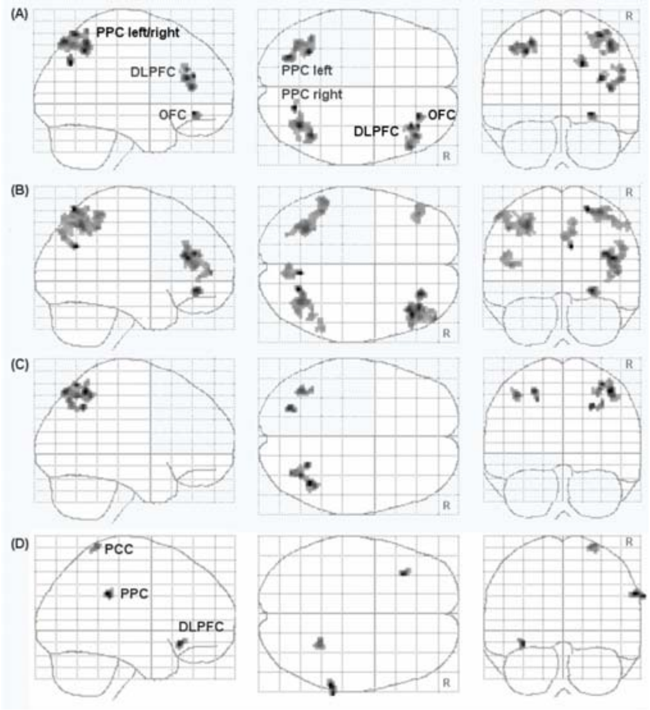

Figure 1. Activated cortical areas. See text for details and explanation.

The analyses also revealed significant differences between the conditions in *sub-cortical areas.* These results are shown in Figure 2. The comparison between social and non-social problems revealed that a significant portion of the dorsal amygdala bilaterally was less activated by the social than by the non-social problems. The comparisons within the social problems revealed a second focus of activation in the ventral portions of the right hemispheric amygdaloid complex and showed relatively lower activity during altruistic in comparison to egoistic and social choices. The bar graphs show that this effect is caused by a decrease of activation in this area, which is elicited by the egoistic responses.

Discussion

We conducted a functional brain imaging study to distinguish the neural correlates of social and non-social decisions and to gain insights in differences of the neural processing of egoistic and altruistic choices. Our materials were a non-monetary version of the Prisoner's Dilemma, which is one of the earliest games developed in game theory (Axelrod, 1984). The paradigm is often used by behavioral scientists to study the roots of cooperation and conflict, between individuals, social groups and even among nations. However, our tasks differ in many respects from other brain imaging studies within the prisoner’s dilemma paradigm. While the studies by Rilling et al. (e.g. 2004) and the majority of behavioral prisoners dilemma studies used a monetary context in which the participants could gain or lose a certain amount of money, in our problems the cost and reward of altruistic and egoistic decisions could not be calculated in terms of monetary units. Instead, the problems consisted of dilemmas in which the participants had to make highly moral or ethical decisions. In this respect our approach builds on the study by Greene et al. (2001). A second difference to other studies is that our problems were carefully piloted and that the context was varied over the entire set of problems, i.e. each problem was embedded into another situation. These "cover stories" were quite realistic: they were presented to the participants as narrative episodes and the participants were requested to play the role of the protagonist.

The imaging data show that a complex neural network of cortical and sub-cortical brain areas is involved in making altruistic or egoistic decisions. The activated cortical brain areas were portions of the orbito-frontal cortex (BA 11, right), the dorsolateral prefrontal cortex (BA 46, right), and the posterior parietal cortex (BA 7, 40, bilaterally). Here an increase of activation was found for social problems and altruistic choices. The sub-cortical brain areas included portions of the amygdala. Here social problems overall resulted in a decrease of activation in the dorsal amygdala whereas the altruistic decisions led to a relative decrease of activation in the ventral portions of the right amygdala.

The most plausible explanation for the increase of activation in the *orbitofrontal cortex (OFC)* during social and altruistic choices is that our participants had to make a decision under conditions in which a conflict of interest occurred and that they thus might have taken into account the potential reward value of the different alternatives of action. With this interpretation we follow the suggestions of Elliott, Dolan, & Frith (2000), who argued that social decisions are based on a feeling of "rightness" and that this is an example of a selection on the basis of the likely reward value (Elliott et al., 2000; p. 308). In fact, our finding is in good agreement with the widely accepted position that the OFC is involved whenever individuals have to generate behavior that is flexible and adaptive rather than "slavishly determined by the current input" (Elliott et al., 2000; p. 308). Many different theories have characterized the OFC as a flexible control system that is involved in executive control (Baddeley, 1986), supervisory attention (Shallice, 1988), and top-down regulation of decision processes (Frith & Dolan, 1997).

The reliance of social and altruistic choices on the *dorsolateral prefrontal cortex (DLPFC)* could reflect the role of this area in overriding the emotional bias to make a selfish choice and in a down-regulating mechanism of emotional responses as described by Blair et al. (2007). This account is consistent with evidence showing that the DLPFC is involved in the execution of cognitive control and response inhibition (Aron, Robbins, & Poldrack, 2004). Many studies have shown that the DLPFC is active when a task requires individuals to suppress an action or if in a Stroop task they have to inhibit reading while naming the color in which a word is written (Bush et al., 1998). In the present context it is also important to mention that other studies have shown that the DLPFC is involved when people must control their thoughts or memories (Bunge, Ochsner, Desmond, Glover, & Gabrieli, 2001). The study by Spitzer et al. (2007) in which individuals' norm compliance was positive correlated with activations in the right DLPFC (and the OFC) points in this direction. Greene et al. (2004) in their study on the neural bases of cognitive control in moral judgments, found increased activity in DLPFC when a moral dilemma required regulative control to suppress amoral behavior.

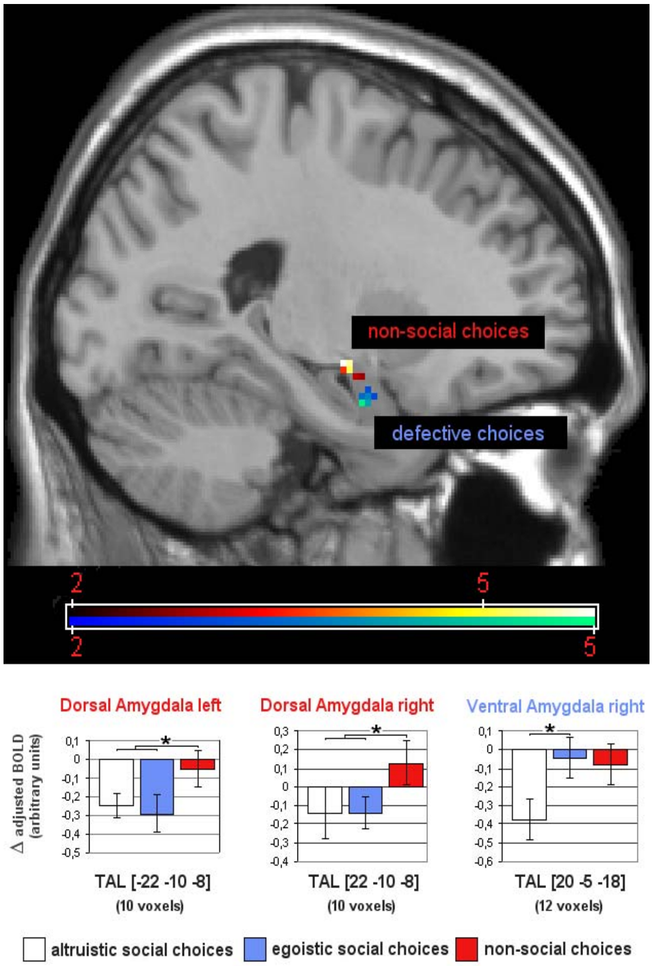

Figure 2: Activated sub-cortical areas. See text for details and explanation.

The findings of our region of interest analysis in the *amygdala* might also have to do with the down-regulating of negative emotion (Blair et al., 2007). We found decreased activation in bilateral dorsal portions of the amygdala during social choices and decreased activation in ventral portions of the right amygdala during altruistic choices. This is in agreement with several neuroimaging studies examining the neural correlates of the cognitive control of emotion (e.g. Levesque et al., 2003). Similar to the cognitive control that is mediated by prefrontal areas Ochsner and colleagues proposed a theory in which the emotion-modulatory effects are based on the interactions between cognitive control processes in prefrontal (and cingulate regions) and emotional processes of reappraisal implemented in multiple emotion-related brain areas, including the amygdala (Ochsner & Feldmann Barrett, 2002). The present findings agree with this view and also fit nicely with other neuroimaging studies that found increased prefrontal and decreased amygdala activation in problems in which the individuals were required to reappraise and to down-regulate negative emotion (Ochsner et al. 2002).

The differential activation in the *posterior parietal cortex (PPC)* is difficult to explain. One problem is that the PPC is a large area that encompasses numerous functions (see the overview in Cabeza & Nyberg, 2000). It has been related visual mental imagery (Knauff, Kassubek, Mulack, & Greenlee, 2000; Ganis, Thompson, & Kosslyn, 2005), working memory (e.g. Smith & Jonides, 1998), and deductive reasoning (Knauff, Mulack, Kassubek, Salih, & Greenlee, 2002; Knauff, Fangmeier, Ruff, & Johnson-Laird, 2003; Fangmeier, Knauff, Ruff, & Sloutsky (2006). Another problem is that particular areas in the PPC show task-independent activity in the so-called “resting-state”. Some authors have argued that this activity might reflect a baseline of brain function involving a specific set of mental operations (Raichle & Snyder, 2007). As the PPC is well-known to be involved in visuo-spatial processing and the representation of the visual periphery, it has been argued that measured activity in PC could simply be “associated with the representation of the world around us” (Gusnard & Raichle, 2001; p. 690). However, other authors have strongly argued against the assumptions that are generally made in accepting the importance of the “default mode”. These authors question the value of studies of the resting state and argue that the idea of “meaningless” default mode has little utility (Morcom & Fletcher, 2007).

How can altruism be achieved? One corollary from the present study is that emotional and cognitive processes must work closely together in suppressing the spontaneous tendency of the egoistic organism that “naturally” tends to behave selfishly and to promote its own interests. A second corollary is that Richard Dawkins might be right when he advises “Let us try to teach generosity and altruism … because we are born selfish”.1 If, as our study suggests, altruism and cooperation is based on learning and experience it is an open question how social life will be altered if on a longer term egoism is rewarded instead of being punished.

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Appendix

Magnetic resonance imaging were performed with a 1.5 Tesla scanner (Magnetom Sonata, Siemens, Erlangen, Germany) equipped with an echo-planar imaging (EPI) booster for fast gradient switching and a parallel 8-channel radio-frequency (RF) receive-transmit headcoil (MRI-Devices Europe, Würzburg, Germany). High-resolution, sagittal T1-weighted images were acquired with an MP-RAGE (magnetization prepared, rapid acquisition gradient echo) sequence to obtain a 3D anatomical scan of the head and brain. Functional imaging was performed with T2*-weighted gradient echo-planar imaging (EPI). The time to echo corresponded to TE = 50 ms, total scan repetition time was TR = 3 sec, the flip angle corresponded to 90°, and we used a field of view FOV = 192 mm, with an isotropic voxel size of 3 □ 3 □ 3 mm. We acquired volumes with 34 contiguous slices and a distance factor of 0-10%. The acquisition sequence of the slices was interleaved. The slices were rotated approximately 10° relative to the AC-PC line; thereby allowing us to image the entire neocortex. The stimulation protocol consisted of 3 runs with 302 volumes each.

The preprocessing and statistical analyses of the data was performed using SPM2 (2002). The functional images were corrected for acquisition delay (slice timing), and realigned. The structural image was co-registered with the functional series and normalized to the MNI152 template. Subsequently, the functional images were normalized and smoothed with a FWHM of 8 mm. Statistical analyses was conducted using a general linear model with a block design, modeling each class of the episodes (social-egoistic, social-altruistic, non-social) with a separate regressor. The regressor was composed of the presentation of the passage "dilemma" as a box car function which was convolved with the canonical HRF function and its time derivatives. Low frequencies confounds were excluded from the model with a high-pass filter of 128 seconds, and the auto regression AR (1) excluded the variance explained by the previous scan.

For the statistical inference we contrasted social against non-social episodes, altruistic choices against non-social problems, egoistic choices against non-social problems, and altruistic against egoistic choices. A contrast image was made for each of the participants and contrasts. These images were used for the random effects analysis on 2nd level. The contrast images (Figure 2A-C) were initially thresholded with $p = 0.001$ (uncorrected for multiple comparisons). Clusters surpassing a threshold of $p \leq 0.05$ (corrected for multiple comparisons) were considered as significantly activated. To complement the results we extracted beta values of all subjects for the three neocortical areas (PPC, DLPFC, OFC) which resulted from the comparison social- vs. non-social choices and for two sub-cortical areas (amygdala left, right) which we derived from the present literature (Adolphs, Tranel, & Damasio, 1998; Adolphs, 2003).

For the region of interest analysis (ROI analysis) in the amygdala we first used the PickAtlas software toolbox (Lancaster et al., 2000; Maldjian, Laurienti, Kraft, & Burdette, 2003). Then the analysis was conducted a second order analysis within SPM2 (theshold $p = 0.01$; family wise error; corrected for multiple comparisons; voxel-level). The different portions of the dorsal and the ventral amygdala were found in two different contrasts. The cluster in the dorsal amygdala was found in the contrast non-social choices versus social choices and the cluster in the ventral amygdala was found in the contrast egoistic social choices versus altruistic social choices. The peak voxels of the ventral and the dorsal amygdala were not identical and the two clusters did not overlap.

In order to analyze the different ROIs within the amygdala we first determined the size of the dorsal and ventral cluster within the amygdala (10 voxels and 12 voxels, respectively). The shape of the ROI was that of the activated cluster itself. Then, we extracted the beta values for each voxel in the dorsal and the ventral cluster and for each condition (altruistic social, egoistic social and non-social) separately. Finally, the beta values were analyzed within the statistical software packaged SPSS. Differences between the conditions for each cluster were analyzed with the paired t-test (df = 9).