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FACULTY OF APPLIED ECONOMICS

DEPARTMENT OF MANAGEMENT

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University of Antwerp, City Campus, Prinsstraat 13, B-2000 Antwerp, Belgium
Research Administration – room B.213
phone: (32) 3 220 40 32
fax: (32) 3 220 47 99
e-mail: joeri.nys@ua.ac.be

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D/2008/1169/016

Comparing the neural basis of mixed-motive versus coordination games in people with different social preferences, an fMRI study

Griet Emonds,[1,*] Carolyn H. Declerck,[1] Christophe Boone,[1] Everhard J.M. Vandervliet,[2] Paul M. Parizel,[2]

[1]University of Antwerp, Faculty of Applied Economics, Department of Management, Prinsstraat 13, 2000 Antwerpen, Belgium

[2]Antwerp University hospital (UZA) and University of Antwerp, Faculty of Medicine, Wilrijkstraat 10, 2650 Edegem, Belgium

* Corresponding author. University of Antwerp, Faculty of Applied Economics, Department of Management, Prinsstraat 13, 2000 Antwerpen, Belgium. Tel: +32 3 275 50 95.

E-mail address: Griet.Emonds@ua.ac.be (G. Emonds)

Abstract

We use fMRI to investigate the neurological correlates of two factors that are known to enhance cooperative strategies in social dilemmas: the provision of extrinsic cooperative incentives, and the intrinsic motivation to cooperate. The former is achieved by changing the pay-off matrix of a mixed motive game (e.g., a Prisoner's Dilemma, PD) to a coordination game (CG). The latter is achieved by comparing people who differ along the personality trait Social Value Orientation. Previous studies have indicated that proself oriented individuals ("hawks") adopt a competitive strategy in a PD but switch to a cooperative strategy in a CG, while prosocial individuals ("doves") maintain high levels of cooperation across games. A major aim of this study is to examine if there are fundamental neurological differences between prosocials and proselfs that substantiate these different behavioral strategies. Our imaging data of a full brain analysis contrasting PD and CG confirm that the PD poses a conflict (increased ACC activation) and induces subjects to think about the possible consequences for self and others (more prefrontal cortex activity). More importantly, a region of interest analysis contrasting prosocials and proselfs suggests that proselfs' strategies are driven by calculation and self-interest. Increased activation was found in the precuneus, DLPFC, the posterior STS, and caudate nucleus. Prosocials' strategies reflect norm compliance, morality, and social interaction. Increased activation was found in the lateral orbotifrontal cortex and the social brain network (including the ventromedial cortex, anterior STS, inferior parietal lobule, and amygdala).

Introduction

Much experimental research in different scientific domains has been devoted to understanding the strategies people use in social dilemmas or mixed motive games. Social dilemmas are uncertain, interdependent situations where people face a choice between a self-serving versus a cooperative strategy. The latter provides mutual benefits, but at a personal cost. If, however, no one cooperates, the outcome of the dilemma is worse for everyone (Dawes and Messick, 2000). Thus, social dilemmas provide a temptation to free-ride on other's cooperation, but at the risk of loosing potential gains from a mutually beneficial relationship.

Understanding how decisions are made in social dilemmas has been approached from different angles. First, behavioral economists have emphasized the importance of *extrinsic* incentives to drive cooperative behavior. Often they study behavior in laboratory games such as the well known PD game, where each person's pay-off is determined by the joint outcome of each person's decision to cooperate or defect. In this game, motives of fear and greed are both present. While mutual cooperation is collectively the best choice, a greedy person can always obtain a better outcome by defecting. Anticipating this, a cooperative but fearful person too will defect. Therefore, many game theorists have investigated ways to transform incentive structures of economic games in order to make cooperation appealing (reviewed in Bornstein, 2003). For example, by decreasing the payoff from defection in a PD to or below the level of the payoff from mutual cooperation, one generates incentives to cooperate. While decision-making still yields an uncertain outcome, the motives of fear and greed are removed and the game becomes one of coordinating on each other's decision. Typically, in line with the prediction of rational choice theory, more mutual coordination on the most cooperative option is found in CG compared to PD games (Kollock, 1998).

Second, social psychologists have traditionally paid attention to the fact that people vary in their tendencies to value cooperativeness and hence in their *intrinsic* motives to behave cooperatively (see also Fehr and Fischbacher, 2002). Specifically, they have identified a stable personality trait, called Social Value Orientation (SVO), referring to people's self- versus other regarding preferences (e.g. Van Lange, 2000). As this trait also reflects how people evaluate interdependent outcomes for self and others (Messick and McClintock, 1968), it can be considered an important determinant of cooperative motives, strategies, and choice behavior (Kollock, 1998; McClintock and Van Avermaet, 1982). Much research has indicated that people with a prosocial value orientation are intrinsically willing to cooperate in a social dilemma, as long as their partners cooperate as well. Using the terminology of evolutionary game theory, prosocials tend to rely on a "dove strategy," opting for the most mutually beneficial outcome. On the other hand, people with an individualistic or competitive orientation (proselfs), tend to rely on a "hawk" strategy, choosing to outperform the others and, hence, not cooperate in a PD. However, proselfs can still be induced to cooperate in a social dilemma when there are extrinsic incentives that make cooperation rewarding, like in a CG (Bogaert et al., 2008). In fact comparing the behavior of prosocials and proselfs in a PD and a CG, Simpson reported that only proselfs adapted their behavior towards more cooperation in the CG and more defection in a PD (Simpson, 2004). Prosocials, on the other hand, played a PD as if it were a CG: they maintain a high level of cooperation in both games.

Third, the neural correlates of decision-making in social dilemmas are gaining increasing attention. However, most studies compare the neural correlates of cooperative versus competitive decisions, ignoring the effect of different incentive structures of the game (Decety et al., 2004; Rilling et al., 2002; Rilling et al., 2004). Moreover, few studies have looked at the simultaneous impact of individual differences in personality on brain activation during social

decision-making in general (but see Spitzer et al., 2007 for an exception). However, we think that to better understand the nature of cooperative decision-making in social interactions, an explicit comparative approach analyzing how the brains of individuals with opposing intrinsic social motives process alternative extrinsic incentive structures might be particularly revealing. Therefore, in this study we investigate the effect of personality as well as incentive structures on social decision-making under uncertainty. Specifically, we investigate first how the neural basis of social decision-making in interdependent situations (characterized by an uncertain outcome) differs in the presence of weak (as in a PD) versus strong extrinsic cooperative incentives (as in a CG). Because we know that people with different social value orientations are differentially affected by these incentive structures, we further compare the neural correlates of decision-making in these games for prosocials and proselfs. A major aim of this study therefore is to investigate if there are fundamental neurological differences between prosocials and proselfs which can account for their behavioral differences that have been observed in social dilemmas. In other words, we ask the question if the changes in the level of cooperation associated with game transformation observed in proselfs, but not in prosocials, can be substantiated by fundamental differences in their neurological underpinnings.

Based on current knowledge of how social dilemmas can be solved and the growing literature on the neural basis of intrinsic and extrinsic motivators during social and strategic decision-making, we have developed specific hypotheses with regards to how brain activation might differ for games with weak versus strong cooperative incentives, played by people with a prosocial versus a proself orientation.

A first stylized fact with respect to strategic decision-making in social dilemmas is that people cooperate less when extrinsic motivation is weak and when intrinsic motivation is hampered by

either the temptation to free-ride, or the fear of betrayal. Thus, when contrasting the neural activity during a CG and a PD, we expect that the higher level of uncertainty associated with the incentive structure of the latter will activate conflict regions in the brain, such as the anterior cingulate gyrus. Consequently, more prefrontal cortex activity is also expected in the PD, corresponding to attempts to solve the dilemma (e.g., McCabe et al., 2001).

A second stylized fact is that proselfs are more motivated by extrinsic rewards (Bogaert et al., 2008). Because their main concern is to obtain the best outcome for themselves, regardless of the type of situation, proselfs tend to defect in PD situations and cooperate in CG. Thus, proselfs' decision-making style is calculative, maximizing personal benefit. With regards to brain activation, we therefore expect that proselfs, regardless of the type of game, will show more activation in regions associated with self-referencing and with calculating rewards compared to prosocials. A brain region which has recently been implicated in self-referencing is the precuneus (BA 31). Reviewing the evidence on the role of the precuneus in processing self-related information, Cavanna and Trimble suggest that this section of the medial parietal cortex "is involved in assigning first-person perspective (the viewpoint of observing the self) and interpreting an action as being controlled by oneself versus another person" (Cavanna and Trimble, 2006, p. 576). Furthermore, we expect proselfs to show more activation in the dorsolateral prefrontal cortex (DLPFC). This region in the frontal lobes has repeatedly been identified as playing a major role in working memory and the type of executive functions needed to solve dilemma-type situations. For example, in an fMRI study by Sanfey et al. (2003) investigating the Ultimatum Game[1], more DLPFC activity was observed when people made the

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[1] In an Ultimatum Game, one player makes an offer to a second player on how to divide a sum of money. The latter can accept or reject the proposal. Rejection leaves both players with nothing, in the other case, the proposal is implemented. Standard economic theory of self-interest predicts that both players are rational, caring only about their own earnings,

rational choice decision, i.e. the smallest offer possible (corresponding to the Nash equilibrium). Finally, we predict that proselfs will show more activation in regions related to the dopamine (DA) reward system, especially the caudate nucleus, an area which is activated upon contingency between an action and a reward. An fMRI study by Spitzer et al. (2007) showed more activation in the caudate nucleus when a person was in a situation where it was possible to either increase the chance to gain money or decrease the chance to loose money.

The third stylized fact on which our predictions are based concerns the behavior of prosocials. While they may be less dependent on extrinsic rewards, their intrinsic motivation to cooperate is conditional upon their expectations that their partners will reciprocate their cooperative acts (Fehr et al., 2005; Simpson, 2004). Because they aspire an equal outcome for themselves and their partner, we hypothesize that their decision-making style is characterized by more perspective taking and social intelligence. Brothers and Ring (1992) and Baron-Cohen et al.(2000; 1999) have identified a "social brain" network which includes regions of the medial frontal cortex, the temporo-parietal junction, and the amygdala. Furthermore, many studies that attempt to locate the neural correlates of morality, perspective-taking, theory of mind skill, and empathy, have pointed to the role of the superior temporal sulcus (STS) and the inferior parietal lobule (IPL) (see e.g., Borg et al., 2006; Decety et al., 2004; Frith and Frith, 2006; Fukui et al., 2006; Greene and Haidt, 2002; Moll et al., 2007). Given the evidence that prosocials have better theory of minds skills and more empathy than proselfs (Declerck and Bogaert, in press), we also expect them to show more activity in some or all of these regions associated with the social brain network. In addition, prosocials may be more norm-compliant because they have internalized social norms associated with cooperation and social responsibility (De Cremer and

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and that therefore the proposer expects the responder to choose anything over receiving nothing and thus accept even the slightest positive amount.

Van Lange, 2001). Spitzer et al. (2007) have associated norm compliance with increased activity in the lateral orbitofrontal cortex (BA 47). Therefore, we also expect this region to show increased activity for prosocials playing dilemma-type games compared to proselfs.

To summarize, we developed two sets of expectations, one for the contrasts of PD versus CG, one for the contrasts between prosocials and proselfs. With respect to the main effect of game incentives, we predict increased ACC and PFC activity in the PD, associated with sensing and solving the conflict. With respect to the main effect of SVO, we expect that proself will show more activity in the precuneus (due to their need for self-referencing), DLPFC (being more calculative), and caudate nucleus (reward-expectancy). On the other hand, prosocials, having more capacity for perspective taking and more norm compliance, will show more activity in the social brain network, consisting of the medial frontal cortex, amygdala, and regions of the temporo-parietal junction (including the STS and IPFL), as well as in the lateral orbitofrontal cortex. Finally we will also explore whether the contrast between prosocials and proselfs is moderated by the type of game.

In order to test these hypotheses, we first perform an exploratory full brain analysis, in which we contrast neural activity for the PD versus the CG, and for proselfs versus prosocials, respectively. We next perform region of interest (ROI) analyses on those regions for the proself-prosocial contrast for which we developed the specific hypotheses listed above.

Materials & Methods

Experimental design

The study was conducted in a blocked design with 3 different conditions, each one separated by a brief rest: a PD, a CG, and a control condition. The two games in the first two conditions make up the within-subject factor of our 2x2 factorial design. The between-subject factor then consists of the proself or prosocial orientation of the participants.

The two games were explained to participants as one single investment game (without differentiating between the PD and the CG conditions) in which each of two players is confronted with the choices to invest or not, representing respectively the options to 'cooperate' and 'defect' described in the introduction. Fig. 1a and 1b represent two possible decision pay-off matrices as shown under the scanner. Rows correspond to decision of the participant (denoted "I"), and columns correspond to the decisions of the other player (denoted by "person" followed by a number). The numbers in each of the four boxes represent the participant's pay-off for the combination of choices made by him/her-self and the other person. The pay-off for the other person is shown in parentheses. In the CG (fig. 1a), most points are earned if both the participant ("I") and the other player invest. While a minimum of trust in the other player's decision is required, the knowledge that "invest" yields the highest pay-off for one self as well as for the other person forms an extrinsic incentive to cooperate.

In the PD game (fig. 1b) the extrinsic incentives are replaced by mixed motives. In this case, "not investing" indicates either that the player is greedy, hoping to benefit from the other person's investment, or that he/she is afraid of betrayal. From an economic viewpoint, "not investing" is

the best option (the Nash equilibrium): you win if the other player invests, and you don't lose anything if the other player doesn't invest. However, this option is collectively deficient, as the best mutual outcome can only be reached if both players invest.

In order to avoid boredom or habituation during the course of the experiment, the pay-offs of the games were varied, yielding a total of 4 different matrices for each game. In the control condition[2] (fig. 1c) participants viewed a number and were asked to indicate whether this was an even or an odd number. During the periods of rest an empty matrix was shown (fig. 1d).

a) Coordination Game (CG)

b) Prisoner's Dilemma Game (PD)

c) Control Condition
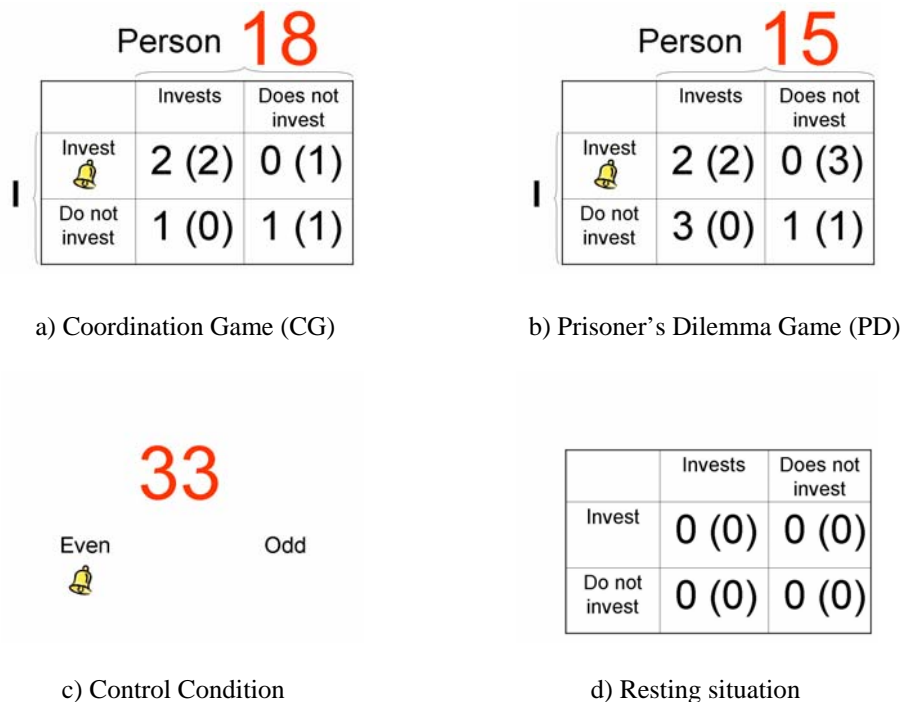
d) Resting situation

Fig. 1: Examples of each of the three conditions used in the design, plus the resting situation, as shown to the subjects inside the scanner. Numbers refer to points that can be earned for each possible outcomes (in parentheses are points earned by the other player). The image of the bell reminds participants for which choice they should push the button and for which they shouldn't. The number above the matrix in the PD and CG condition corresponds to the partner with which the participant is coupled for this interaction.

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[2] For the sake of brevity, the contrasts between game conditions and control conditions will not be presented in this paper. Interested readers are welcome to contact the corresponding author.

Each block lasted for 30 seconds, during which 4 different matrices with the same game structure (PD or CG) were shown (or 5 different numbers for the control condition). There were 7 cycles of random PD-CG-Control block alternation. Each block was always followed by a 30 sec resting period. The total scanning time for acquiring the functional data was 21 minutes.

Participants

Participants were recruited at the University of Antwerp through e-mail and web-based announcements. Monetary incentives were emphasized. All right-handed candidates[3] were asked to fill in two forms on our website, the first comprising a medical screening to make sure that they were suited to undergo an MRI scan at 1,5 Tesla, and the other one to determine their Social Value Orientation (SVO) by means of the decomposed games measure (Van Lange, 2000). Each of the 9 items in this task contains three alternative outcome distributions of points allocated to oneself and to an anonymous other. The three possible outcome distributions represent a particular orientation. By completing the task, participants thus classify themselves as having a prosocial, individualistic, or competitive orientation when at least six out of nine choices are consistent with one of these three orientations. In our study, we only selected those candidates who scored nine out of nine for either the prosocial or the individualistic orientation. We refer to the latter as the "proself" orientation, which differs slightly from conventional nomenclature where the individualistic and the competitive orientations are combined and called proself.

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[3] Candidates who indicated that they were ambivalent about their handedness were asked to fill in a questionnaire (translated and adapted from Oldfield, R.C., 1971. Assessment and Analysis of Handedness - Edinburgh Inventory. Neuropsychologia 9, 97-113.). Based on this assessment, one candidate was still allowed to participate in the study.

Candidates who were medically eligible to participate in the fMRI study and who were found to have a completely consistent SVO were contacted by mail and invited to a scanning session that took place in the summer of 2007 at the Antwerp University Hospital (Universitair Ziekenhuis Antwerpen (UZA), Edegem). This study and all procedures were approved by the Commission of Medical Ethics at the University of Antwerp.

Twenty-eight subjects (15 prosocials and 13 proselfs, mean age = 24.4 years, ranging from 19 to 33 years) participated. None of the participants had a history of neurological or psychiatric illness, were on any medication, or suffered from claustrophobia. Behavioral data was obtained for all participants. However, due to technical problems with the scanner, the fMRI images of 4 participants were not measured correctly and these subjects therefore had to be excluded from the fMRI data analysis. One subject showed unusually large ventricles, and this dataset was therefore also excluded. Eventually, 12 prosocials and 11 proselfs were included for the fMRI data analysis, 13 males and 10 females (mean age = 24.1 years, ranging from 19 to 33 years).

Procedures

Subjects arrived at the hospital and were told they would participate in a study investigating which parts of the brain are involved when making economic decisions. The written experimental procedures explained that participants would be playing an investment game 56 consecutive times while under the scanner. For each game they would be matched with a different partner who would be identified by a number (see fig. 1a and 1b). They were to make one single decision per game: to invest or not. The combination of their decision and that of their partner would determine how many points were gained or lost for that particular game. Each point had

a real monetary value of 10 Eurocents. Each participant's earnings (or losses) were added (or subtracted) to an initial 10 Euro show-up fee.

The instructions further explained that, for practical reasons, not all the game partners could be actually present in the laboratory, but that these people had already (one by one) gone through the same procedure at an earlier time. The answers they had then given were going to be used now and matched with the answers of the current participant. In reality participants' answers were matched to a series of random answers (50/50). The participants' answers thus influenced the amount of money they earned, but these earnings were independent of any other player. Comparable procedures have been used by other authors in the field, e.g. Sanfey et al. (2003), Rilling et al. (2004).

Subsequently, participants viewed a series of photographs of their alleged future partners, without any names or numbering to preserve anonymity and to prevent that participants would think back to a specific picture during the actual experiment. Thus there was no way anyone under the scanner could link the numbers representing the different partners to actual people. The numbers used in the actual games were only meant to emphasize that every game was a single social interaction with one of the individuals they had previously viewed on the photographs. To add credibility to this procedure, each participant was asked whether their picture could be taken as well and used together with their own answers to serve as partner for future participants.

The written instructions included two practice-games with 16 confirmation questions. After answering all questions correctly, participants played one last practice round on a laptop to

experience the decision time they would be allotted during the actual experiment. The control and resting conditions were at that time also explained.

fMRI Experiment

Participants lay down on the scanner table and wore headphones to reduce the noise. Some pressure was applied on the headphones by the head coil, to minimize motion artifacts. A mirror was mounted on top of the head coil, so that participants could view the projections on a screen positioned behind the scanner.

During the experiment, participants used a push-button to indicate their decisions. These answers were manually recorded and combined with the answers of the alleged partners, which were kept constant for every participant. The average earnings comprised 19.31 Euro.

Image acquisition

First, anatomical images were acquired using a 1,5 Tesla Siemens Sonata scanner and CP head coil (Siemens, Erlangen Germany). A T_1-weighted MP-RAGE protocol was used (256 x 256 matrix, 176 1 mm sagittal slices, FOV = 256 mm). During the same session, functional images were acquired using T_2*-weighted EPI (TR = 3000 ms, TE = 50 ms, 384 x 384 image resolution, FOV = 192 mm, 35 4 mm slices without gap, voxel size = 3 x 3 x 4 mm^3).

Data analysis

Behavioral data were analyzed using SPSS (SPSS for Windows, Rel. 14.0.1, 2005, Chicago: SPSS Inc.). Image analysis was conducted with BrainVoyager QX (v 1.9.9, BrainInnovation,

Maastricht, The Netherlands). Images were preprocessed by means of slice time correction using sinc interpolation, 3D motion correction using trilinear/sinc interpolation, space domain 3D spatial smoothing with 4 mm FWHM Gaussian kernel, temporal smoothing in 3D with a high pass filter of 3 cycles in time course, and linear trend removal. An iso-voxel step resized the functional voxels to a 3 x 3 x 3 mm configuration. For spatial normalization of the images, the standard 9 parameter landmark method of Talairach and Tournoux, implemented in BrainVoyager, was used (Talairach et al., 1988).

For each participant, a general linear model (GLM) was created with the percent BOLD signal change as dependent variable, and with 9 regressors: PD, CG, control condition, and 6 regressors correcting for motion (translation and rotation, each in 3 directions). All regressors were convolved with a standard gamma model of the hemodynamic impulse-response function. Subsequently, for every participant, at every voxel in the brain, a contrast was calculated between regression coefficients of interest. To determine where the average contrast values for the group as a whole differed significantly from zero, one-sample t tests were performed, contrasting PD versus CG, focusing on the main effect of the type of game, and proselfs versus prosocials, focusing on the main effect of individual differences in SVO.

All whole-brain statistical maps were corrected for multiple comparisons using cluster size thresholding (Forman et al., 1995; Goebel et al., 2006). The initial voxel-level (uncorrected) threshold was set at $p < 0.01$. Then thresholded maps were submitted to a whole-brain correction criterion based on the estimate of the map's spatial smoothness. After a procedure of 1000 iterations (Monte Carlo simulation) for estimating cluster-level false-positive rates, a minimum cluster-size threshold of 189 anatomical voxels, that yields a cluster-level false-positive rate of 5%, was applied to the statistical maps.

For the main contrast between Proselfs and Prosocials, not one region survived the stringent multiple comparisons correction. Because we had a priori hypotheses regarding specific brain regions that would be detected in this contrast, we followed the example of studies by Van Opstal et al. (2008) and Wright et al. (2008) and removed the cluster threshold, accepting contrast values as significantly different from zero when $p < 0.01$. In order to be absolutely certain that none of the clusters we identified in this manner would turn out to be a false positive, we performed additional ROI analyses on every cluster for which we developed a hypothesis in the introduction. ROI analyses revealing clusters with significant contrast values increase our confidence that the activation truly reflects a main effect of SVO.

Results

Behavioral data

Consistent with previously published results, the behavioral data obtained from our sample showed more cooperation in the CG than in the PD ($t = 3.983$, $p < 0.001$) (e.g., Erev et al., 1993; Harrison and Hirshleifer, 1989; Kiyonari et al., 2000; Simpson, 2004). This finding holds when considering only the proself individuals ($Z = -2.608$, $p = 0.009$). For prosocials, however, the difference between games did not reach significance ($Z = -1.786$, $p = 0.74$). All behavioral results are illustrated in fig. 2. Significant effects of SVO were not detected, probably due to the small sample size.
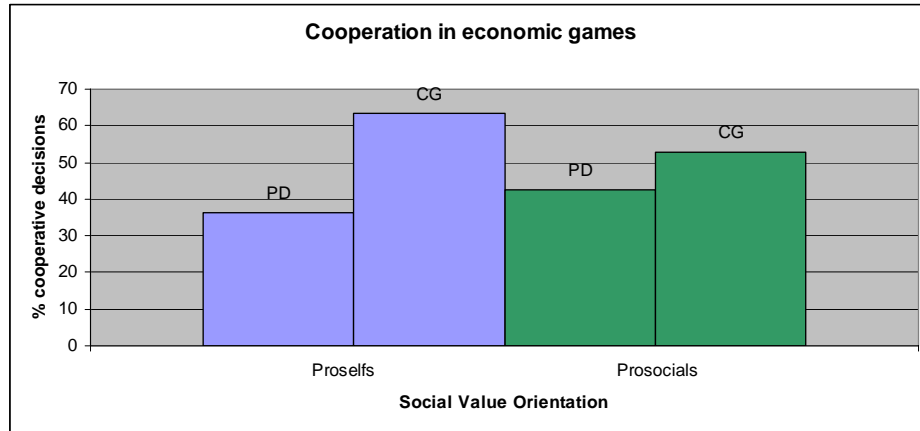
16

Fig. 2: Percentage of cooperative decisions made by proselfs and prosocials in Prisoner's Dilemma games (PD) and Coordination Games (CG). Overall there is more cooperation in the CG (t = 3.983 with p = 0.001). This difference only holds among the proselfs (Z = -2.608 with p = 0.009), not among prosocials (Z = -1.786 with p = 0.74). The main effects of SVO did not reach significance.

fMRI data

Results of the contrast PD versus CG for the whole brain are shown in table 1. Student-t values for all regions yielding significant differences in activation are reported. A main effect of game incentives was detected in the dorsal ACC (BA 32), with more activation in PD compared to CG. In line with our hypotheses, we also found significant differences in the PFC (BA 8, 9, 10, 44 and 46).

With regards to the contrast between prosocials and proselfs, we test the specific hypotheses which we developed in the introduction. As predicted, the full brain analysis (without multiple comparisons corrections (see also Van Opstal et al., 2008; Wright et al., 2008)) detects more activation for proselfs in the precuneus (BA 31), caudate nucleus and DLPFC (BA 9). Unlike predicted, proselfs also show more activation in the posterior STS (BA 39) Among prosocials the

anterior STS (BA 22), IPL (BA 40), VMPFC (BA 10) and amygdala are activated more, all

regions associated with a "social brain" network. We also find more activation of BA 47 in

prosocials. The results of this analysis are shown in the left side of table 2.

Table 1
Main effect of game structure on decision making in social dilemmas (PD versus CG).

Region	BA	Side	X	Y	Z	Size	T(22)
Frontal Lobe							
Inferior Frontal Gyrus	44	R	50	13	19	287	4.941
Middle Frontal Gyrus	6	L	-30	-1	49	557	4.606
		R	28	3	49	1752	5.447
	8	L	-30	24	39	809	5.169
		R	45	10	38	262	4.442
	9	L	-28	29	34	625	4.709
		R	44	31	27	962	4.675
	10	R	26	53	20	935	4.996
	46	L	-38	44	5	374	5.386
		R	46	21	24	397	4.571
Medial Frontal Gyrus	8	R	2	18	44	1453	5.098
	32	L	-3	9	46	1079	5.268
Superior Frontal Gyrus	6	L	-1	7	48	895	4.771
	8	R	21	23	50	241	3.763
	9	R	43	35	26	869	4.675
	10	L	-28	46	20	942	5.728
Precentral Gyrus	4	L	-35	-25	54	360	-4.620
	9	L	-39	21	40	261	5.169
		R	36	5	32	214	3.954
Sub-Gyral	6	L	-20	5	54	1055	4.607
		R	17	0	51	1488	5.676
Temporal Lobe							
Middle Temporal Gyrus	19	L	-36	-75	20	324	5.206
Superior Temporal Gyrus	39	R	51	-56	22	828	6.124
Supramarginal Gyrus	40	L	-51	-50	20	574	4.527
Fusiform Gyrus	37	L	-42	-57	-13	430	4.627
Parietal Lobe							
Precuneus	7	L	-17	-72	50	455	4.808
		R	4	-53	41	1994	5.623
	19	R	32	-71	37	692	5.050
Inferior Parietal Lobule	39	L	-38	-66	40	389	3.681
	40	R	37	-48	38	915	4.997
Superior Parietal Lobule	7	L	-25	-67	49	848	4.439
Supramarginal Gyrus	40	R	49	-47	30	568	4.406
Occipital Lobe							
Middle Temporal Gyrus	19	R	37	-63	12	241	5.145
Limbic Lobe							
Cingulate Gyrus	31	L	-8	-42	45	158	3.645
		R	6	-46	40	633	5.623
Sub-lobar							
Thalamus, pulvinar		L	-8,	-29	4	446	4.335
Thalamus, ventral anterior nucleus		L	-15	-5	9	439	4.977
Thalamus		L	-7	-28	-2	323	4.335
		R	10	-13	13	1025	4.634
Midbrain							
Red Nucleus		R	6	-16	-8	212	4.567

Resulting t-values from whole-brain multi-subject GLM analysis with contrast PD-CG ($t_{(22)}$, corrected $p < 0.05$, R =

189). Positive t-values refer to more activation in the PD compared to the coordination game. Negative t-values

refer to more activation in the coordination game. BA = Brodmann area; PD = Prisoner's Dilemma; CG =

Coordination Game; L = left; R = right; size = number of 1 mm³ voxels; scores are taken from the peak voxel of

the cluster; Talairach coordinates of mean voxel of the cluster.

Table 2
Main effect of social value orientation on decision making in social dilemmas (Proselfs (Pse) versus Prosocials (Pso)).

Region	BA	Side	X	Y	Z	Size	$t_{(21)}$	ROI analysis (Pse-Pso) $t_{(21)}$	p
Frontal Lobe									
Inferior Frontal Gyrus	47	R	58	31	-4	22	-3,484	-3.962	0.001
Medial Frontal Gyrus	10	R	12	41	10	1	-2,886	-3.284	0.003
Superior Frontal Gyrus	9	L	-8	56	31	40	3,650	3.789	0.001
Temporal Lobe									
Superior Temporal Gyrus	22	L	-56	3	-2	5	-2,839	-4.194	0.000
		R	48	4	-2	12	-3,102	-3.803	0.001
	39	R	53	-59	31	14	3,029	3.428	0.002
Parietal Lobe									
Inferior Parietal Lobule	40	L	-52	-34	31	82	-3,532	-3.929	0.001
Precuneus	31	L	-9	-55	32	2	2,892	2.992	0.007
Limbic Lobe									
Amygdala		R	27	-7	-14	1	-3,047	-3.496	0.002
Sub-lobar									
Caudate nucleus (body)		L	0	2	13	4	3,277	3.413	0.003

Left side of table: A priori defined regions for which differences between prosocials and proselfs are expected (see introduction) and coordinates of clusters of activation found in these regions through whole-brain multi-subject GLM analysis with contrast Proself - Prosocial ($t_{(21)}$, uncorrected, $p < 0.01$). Right side of the table: ROI analysis (See text for details). t = result of student t-test (degrees of freedom); Positive t-values refer to more activation in Proselfs compared to Prosocials, negative t-values refer to more activation in Prosocials; p = p-value. BA = Brodmann area; L = left; R = right; X, Y, Z = Talairach coordinates of mean voxel of cluster; size = number of 1 mm^3 voxels; Pse = proself; Pso = prosocial; SVO = social value orientation. Scores from whole-brain analysis are taken from the peak voxel of the cluster; scores from ROI analysis are mean for each cluster.

The ROI analysis (right side of table 2) confirms the whole-brain analysis and thus indicates that the detected clusters are all clusters of true activation relevant for the main effect of SVO. With this ROI analysis we included an ANOVA to test for possible interactions between type of game and SVO. None of the ROI's, however, showed a significant interaction effect.

Discussion

The aim of our study was to understand how the brain solves social dilemmas. To accomplish this, an fMRI study was performed to test specific hypotheses with regard to two different parameters of cooperative decision-making in social dilemmas: extrinsic incentives and SVO. First we contrasted brain activation patterns while participants played two economic games with different incentives structures. Next we investigated which brain regions were active when individuals with opposing social motives played these games. With the latter, we hoped to identify fundamental neurological differences between people with a prosocial versus a proself social value orientation which could account for their different pattern of behavior in social dilemmas.

The first set of hypotheses concerned the main effect of game incentives, contrasting a PD game with a CG. Our behavioral data support earlier work reporting more cooperation in a CG compared to a PD (e.g., Erev et al., 1993; Harrison and Hirshleifer, 1989; Kiyonari et al., 2000; Simpson, 2004). To substantiate this finding, we predicted to find increased activation of the ACC and PFC in the PD, associated with sensing and solving the dilemma. Our fMRI data very much agrees with this prediction.

First, our data indicate that the PD yields more dorsal ACC (BA 32) activation. This region was described by Mohanty et al. (2007) as being involved in attention and executive function. Its activation is especially associated with the detection of conflicts occurring between incompatible streams of information. Carter et al. (1999) state it is involved in evaluating these conflicting demands, and signals when and how executive functions subsumed by the DLPFC should be implemented.

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Second, the DLPFC (a part of the PFC that is involved in spatial and conceptual reasoning processes, see Stuss and Levine (2002)) was found to be more activated in the PD game. More specifically, we detected clusters of activation in BA 8, 9, 44 and 46 in this region (see Stuss and Levine, 2002). The activation of BA 9 in particular is interesting considering the study of Fukui et al. (2006) reporting that this region is involved in mentalizing about the self relative to others, and projecting the self into the future.

Third, we also detected a significant effect of the PD in the ventral part of the PFC (BA 46), which is known to play a role in behavioral self-regulation, with an emphasis on tasks in which choices must be made in under-specified situations (Stuss and Levine, 2002). A social dilemma undoubtedly qualifies as such under-specified situation. Spitzer et al. (2007) further associated BA 46 with the mere presence of a social context.

Fourth, the frontal poles (BA 10), the most anterior region of the PFC and presumed to be one of the regions most strongly related to human emotional and social behavior (Stuss and Levine, 2002), also showed more activation in the PD game. Borg et al. (2006) described BA 10 as a region linked with sociality as well as morality, associated with self-referencing during theory of mind tasks, and maintaining long-term goals while more immediate goals are being processed.

Thus, the imaging data in our study confirm that a PD generates conflict, and that mentalizing about the outcomes for self and others (also known as theory of mind) are involved in solving this conflict. Such skills are much less important when the dilemma is replaced by a coordination task.

Our second set of expectations concerned the influence of individual differences in SVO on behavior in social dilemmas. Again, our behavioral data confirm earlier work indicating that the difference in cooperative decision-making between the two games is especially pronounced for individuals with a proself orientation (Simpson, 2004). Because extrinsic incentives are less important for prosocials who have internalized the norm of social responsibility (De Cremer and Van Lange, 2001), they tend to play both games as a social dilemma in which they aspire the best joint outcome. Proselfs, in contrast, use strategies dictated by self-interest and appear to be only motivated to cooperate when extrinsic incentives are present. Therefore, we hypothesized that there may be fundamental neurological differences in the decision-making processes of proselfs and prosocials, which could account for the behavioral transformation of proselfs across the two games, and the typically high level of cooperation of prosocials in both games. In line with this general prediction, our imaging data indicate that prosocials' strategies are more social and norm-abiding, while proselfs are more calculative and motivated by reward. Although none of the main effects of SVO survived the multiple comparisons correction to $p < 0.05$ in the whole brain analysis, we found clusters of activation in almost all of our a priori defined ROI's. These will be discussed in detail next.

For proselfs, we found clusters of increased activation (compared to prosocials) in four ROI's. The first one, the precuneus, has been associated with an intentional self component (agency), mental imagery, and shifting between first and third person perspective taking (Cavanna and Trimble, 2006). The DLPFC (BA 9), our second ROI, is involved with conceptual and calculative reasoning processes, as well as with mentalizing about the self (Fukui et al., 2006; Stuss and Levine, 2002). The third region of activation is the caudate nucleus, which is thought to play a crucial role in processing information about positive and negative reinforcers (Schultz et al., 2003). Previous studies found this region to be activated when a subject can increase his

chances of earning additional money or decrease the probability of losing money by taking appropriate actions (Spitzer et al., 2007; Tricomi et al., 2004). In our study, we interpret the activity detected in the caudate nucleus as indicating that proselfs foster greater expectations about the possibility of getting rewarded compared to prosocials. So far, these results support the view that proselfs are especially interested in positive outcomes for themselves, and that they approach the games in a calculative manner.
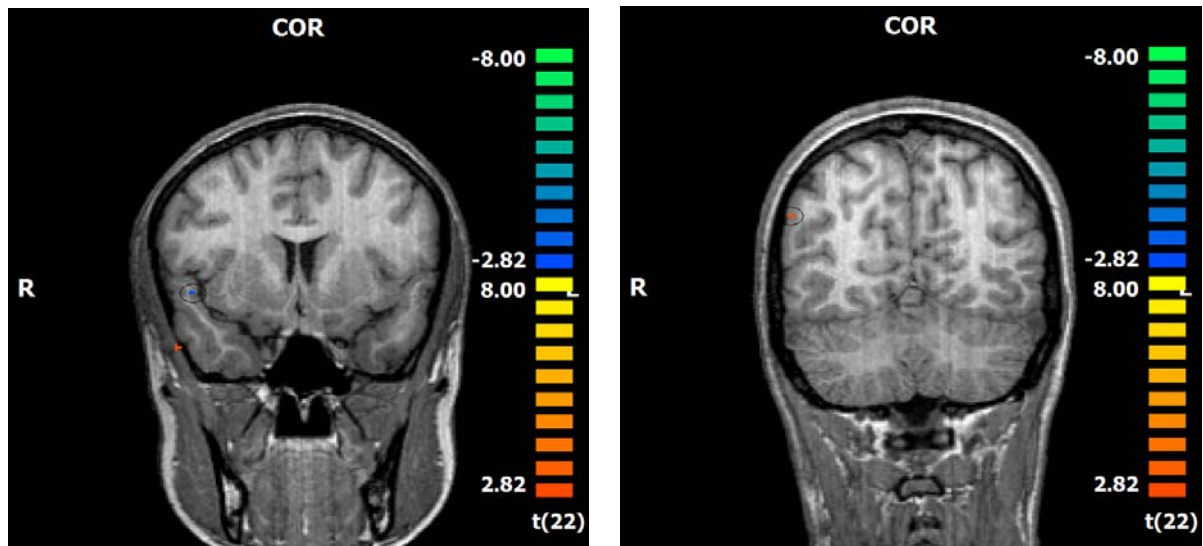

Fig. 3: Significant clusters of activation in whole-brain random effects analysis contrasting proselfs and prosocials (Pse-Pso) after removing cluster size threshold (p < 0.01). Color bar denotes t-values. Left: the contrast showed more activity in the right anterior superior temporal sulcus (STS) (BA 22) in prosocials (encircled). Image sliced at y = 4. Right: in the right posterior STS (BA 39) there was more activity in the proself group compared to the prosocials (encircled). Image sliced at y = -59.

t(22) = t-values from student t-test with 22 degrees of freedom; y = Talairach coordinate; Cor = Coronal view; L = left; R= right.

A fourth region that was found to be more activated in the proselfs was the posterior STS, BA 39 (see right panel of fig. 3), a region which is often implicated in mentalizing (Fukui et al., 2006). Although this was not the direction in which we expected the STS to be activated, it is, in

retrospect, not surprising that perspective taking would be important to proselfs as well. It is, after all, because proselfs understand the perspective of the other player that they realize that a CG yields a cooperative advantage. The insight that the other player irrevocably benefits from cooperation in a CG triggers proselfs to change towards more cooperative behavior in the CG.

For prosocials, the ROI's in which we found clusters of increased activation (relative to the proselfs) include the VPFC (BA 10 and 47), amygdala, the IPL (BA 40), and the STS (BA 22). The VPFC is intimately connected with limbic nuclei involved in emotional processing, like the amygdala, and has been associated with inhibition, emotion, and reward processing (Stuss and Levine, 2002). BA 47 in particular has been associated with the subjective representation of punishment (Kringelbach and Rolls, 2004) and accordingly, with norm compliance (Spitzer et al., 2007). The finding that this region is more activated in prosocials could be an indication that norm compliance, due to the threat of social punishment such as guilt or poor reputation, is an automatic, internalized strategy that surfaces during decision-making in social interaction (Nelissen et al., 2007). Spitzer et al. (2007) also found greater activation of BA 47 in a social economic game condition (interacting against a real person) compared to a non-social one (interacting with a computer). The lateral part of the VPFC has further been implicated in moral judgment tasks. BA 10, in particular, a region related to the formation of episodic memories and the self in general (Tulving, 1985) is involved in sociality and morality, theory of mind tasks, and focusing on one's long-term goals (Borg et al., 2006; Moll et al., 2001).

The higher activation of the amygdala in prosocials could be indicative of a greater need for trust in prosocial's decision-making strategy. As behavioral reciprocators that are willing to initiate cooperation, it is not unlikely that prosocials take on a trusting yet fearful stance. The

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amygdala is known to be one of the regions essential in judging trustworthiness (Winston et al., 2002). Alternatively, it is also possible that the amygdala is activated because it is an essential link in the social brain network ((Baron-Cohen et al., 1999), which we postulate may be dominating the decision-making strategy of prosocials.

The finding that the IPL (BA 40) is more activated in prosocials compared to proselfs also reflects more social awareness during decision-making. Borg et al. (2006), as well as Walter et al. (2005), describe BA 40 as part of a complex heteromodal region associated with the ability to evaluate one's sense of agency with a sense of moral responsibility.

Finally, the anterior STS (BA 22) was also more activated in prosocials compared to proselfs (see left panel of fig. 3). The STS is commonly considered to be part of the network that forms the social brain and is regularly found to play a distinct role in mentalizing (Fukui et al., 2006). The latter authors associate this region with higher cognitive functions needed in social interaction, such as the ability to predict current human behavior based on past experiences and observations. Again, we predicted the STS to be more active in prosocials, based on our general supposition that decision-making in prosocials is driven by activation of the (entire) social brain network. While our findings do not contradict this tenet, only the anterior STS appears more activated in prosocials. As described above, the posterior STS, in contrast, was found to be more activated in the proselfs (activation patterns of both anterior and posterior STS are illustrated in fig. 3). This differentiation between the anterior and posterior STS based on differences in SVO is especially relevant considering Borg et al.'s (2006) reports that the anterior and posterior STS may be functionally distinct. They describe the posterior STS as a region that is especially involved in thought-provoking first-time moral judgment, requiring executive resources. The anterior portion of the STS is more likely to play a role in previously

resolved routine moral judgment that requires more semantically based representational knowledge. This differentiation between posterior and anterior STS is consistent with the results we described above, indicating that proselfs use more cognitive, calculative strategies to solve any dilemma, and that they base their decision on figuring out the "hic und nunc" incentive structure associated with it. Therefore, they must analyze every single game as a situation requiring a "first-time" decision. Prosocials, however, follow their intrinsic motivation throughout the series of games without paying much attention to the external incentives. Once the social brain network is activated, their decision-making strategy is characterized by routine moral judgment.

The imaging results for prosocials support our predictions and indicate that prosocials perceived both PD and CG as social dilemma situations activating the social brain network. Although every one of the regions revealing enhanced activation may by itself be important in determining prosocials' behavior, it would be interesting to investigate in future research whether prosocial strategies are truly the result of the connectivity between these regions. This would support the view that prosocials' intrinsic cooperative motivation is the result of activating an entire social brain network, which extends from the PFC to the temporo-parietal junction and the amygdala in the limbic region.

The fact that the proself-prosocial contrasts did not depend on the type of game (no significant interaction effects) underscores that people with different intrinsic motives approach social interactions in fundamentally different ways. This is also consistent with Simpson's (2004) behavioral findings that proselfs solve a PD as if it were a CG.

One of the limitations of this study is the fact that our a priori hypotheses were based on the literature that is currently available. However, there may be other differences between prosocials and proselfs that we did not address with our ROI's. Furthermore, Because we preferred to use a block design for our particular research questions, we can not draw any conclusions about actual cooperative decisions. It would be interesting to conduct a similar study using an event-related design and put the focus on the neural correlates of cooperative decision making of proselfs versus prosocials.

Conclusion

In conclusion, the imaging data presented in our study corroborate that people with opposing social motives ("hawks" and "doves") rely on fundamentally different strategies to solve a social dilemma, as their brains show different patterns of activation. First of all, our data confirm that a mixed motive game, such as a PD, poses a conflict (activating the ACC), forcing one to think about the consequences of the decision for self and other (activating regions of the prefrontal cortex such as BA 9, 10, 46). Second, our data also confirm that individual differences in social value orientation are an additional influence on the decision making process in CG and PD games. Proselfs approach the games in a rather calculative manner (activating the DLPFC, BA 9), are especially concerned with their own outcome (activating the precuneus) and make decisions that they believe are contingent on obtaining reward or avoiding punishment (activating the caudate nucleus). Therefore, people that rely on such a "hawk" strategy are very sensitive to the presence of either external incentives or mixed motives, and readily adapt their behavior according to the game structure. In this experiment they made clearly different decisions in each of the two games. Prosocials, on the other hand, perceive both games more as social interactions in which a mutually beneficial outcome is the most desirable option. This

appears to activate the entire social brain network (temporo-parietal junction, BA 22, BA 40, medial prefrontal cortex, BA 10, and amygdala). Their decision making process leaves more room for emotional influences (BA 40 and amygdala) and they appear more concerned with issues of morality (BA 10) and social norms (BA 47). People with such a "dove" strategy thus approach social dilemma situations with a strong emphasis on internalized norms which surface during social interaction and with much less attention for external incentives. This explains why their typical behavioral pattern shows little or no difference between their decisions in a mixed motive versus a coordination game. We believe therefore, that the most noteworthy finding in this study resides in the corroborations that (1) the brain engages different neural regions for dilemma and coordination problems, and (2) that "hawks" and "doves" rely on different neural substrates for engaging in such social interactions.

Acknowledgments

References

Baron-Cohen, S., Ring, H.A., Bullmore, E.T., Wheelwright, S., Ashwin, C., Williams, S.C.R., 2000. The amygdala theory of autism. Neuroscience and Biobehavioral Reviews 24, 355-364.

Baron-Cohen, S., Ring, H.A., Wheelwright, S., Bullmore, E.T., Brammer, M.J., Simmons, A., Williams, S.C.R., 1999. Social intelligence in the normal and autistic brain: an fMRI study. European Journal of Neuroscience 11, 1891-1898.

Bogaert, S., Boone, C., Declerck, C.H., 2008. Social Value Orientation and cooperation in social dilemmas: a review and conceptual model. British Journal of Social Psychology 47, 453-480.

Borg, J.S., Hynes, C., Van Horn, J., Grafton, S., Sinnott-Armstrong, W., 2006. consequences, action, and intention as factors in moral judgments: an fMRI investigation. journal of cognitive neuroscience 18, 803-817.

Bornstein, G., 2003. Intergroup conflict: Individual, group, and collective interests. Personality and Social Psychology Review 7, 129-145.

Brothers, L., Ring, B., 1992. A Neuroethological Framework for the Representation of Minds. journal of cognitive neuroscience 4, 107-118.

Carter, C.S., Botvinick, M.M., Cohen, J.D., 1999. The contribution of the anterior cingulate cortex to executive processes in cognition. Reviews in the Neurosciences 10, 49-57.

Cavanna, A.E., Trimble, M.R., 2006. The precuneus: a review of its functional anatomy and behavioural correlates. Brain 129, 564-583.

Dawes, R.M., Messick, D.M., 2000. Social Dilemmas. International Journal of Psychology 25, 111-116.

De Cremer, D., Van Lange, P.A.M., 2001. Why prosocials exhibit greater cooperation than proselfs: The roles of social responsibility and reciprocity. European Journal of Personality 15, S5-S18.

Decety, J., Jackson, P.L., Sommerville, J.A., Chaminade, T., Meltzoff, A.N., 2004. The neural bases of cooperation and competition: an fMRI investigation. NeuroImage 23, 744-751.

Declerck, C.H., Bogaert, S., in press. Social Value Orientation is related to empathy and the ability to "read the mind in the eye". The journal of Social Psychology.

Erev, I., Bornstein, G., Galili, R., 1993. Constructive Intergroup Competition as a Solution to the Free Rider Problem - a Field Experiment. Journal of Experimental Social Psychology 29, 463-478.

Fehr, E., Fischbacher, U., 2002. Why social preferences matter - The impact of non-selfish motives on competition, cooperation and incentives. Economic Journal 112, C1-C33.

Fehr, E., Fischbacher, U., Kosfeld, M., 2005. Neuroeconomic foundations of trust and social preferences: Initial evidence. American Economic Review 95, 346-351.

Forman, S.D., Cohen, J.D., Fitzgerald, M., Eddy, W.F., Mintun, M.A., Noll, D.C., 1995. Improved Assessment of Significant Activation in Functional Magnetic-Resonance-Imaging (Fmri) - Use of a Cluster-Size Threshold. Magnetic Resonance in Medicine 33, 636-647.

Frith, C.D., Frith, U., 2006. How we predict what other people are going to do. Brain Research 1079, 36-46.

Fukui, H., Murai, T., Shinozaki, J., Aso, T., Fukuyama, H., Hayashi, T., Hanakawa, T., 2006. The neural basis of social tactics: An fMRI study. NeuroImage 32, 913-920.

Goebel, R., Esposito, F., Formisano, E., 2006. Analysis of Functional Image Analysis Contest (FIAC) data with BrainVoyager QX: From single-subject to cortically aligned group general linear model analysis and self-organizing group independent component analysis. Human Brain Mapping 27, 392-401.

Greene, J., Haidt, J., 2002. How (and where) does moral judgment work? Trends in Cognitive Sciences 6, 517-523.

Harrison, G.W., Hirshleifer, J., 1989. An Experimental Evaluation of Weakest Link Best Shot Models of Public-Goods. Journal of Political Economy 97, 201-225.

Kiyonari, T., Tanida, S., Yamagishi, T., 2000. Social exchange and reciprocity: confusion or a heuristic? Evolution and Human Behavior 21, 411-427.

Kollock, P., 1998. Social Dilemmas: the anatomy of cooperation. Annual Review of Sociology 24, 183-214.

Kringelbach, M.L., Rolls, E.T., 2004. The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. Progress in Neurobiology 72, 341-372.

McCabe, K., Houser, D., Ryan, L., Smith, V., Trouard, T., 2001. A functional imaging study of cooperation in two-person reciprocal exchange. Proceedings of the National Academy of Sciences of the United States of America 98, 11832-11835.

McClintock, C.G., Van Avermaet, E., 1982. Social values and rules of fairness: A theoretical perspective. In: Derlega, V.J., Grzelak, J.L. (Eds.), Cooperation and helping behavior; Theories and research. Academic Press, New York, pp. 43-71.

Messick, D., McClintock, C.G., 1968. Motivational bases of choice in experimental games. Journal of Experimental Social Psychology 4, 1-25.

Mohanty, A., Engels, A.S., Herrington, J.D., Heller, W., Ho, M.H.R., Banich, M.T., Webb, A.G., Warren, S.L., Miller, G.A., 2007. Differential engagement of anterior cingulate cortex subdivisions for cognitive and emotional function. Psychophysiology 44, 343-351.

Moll, J., de Oliveira-Souza, R., Garrido, G.J., Bramati, I.E., Caparelli-Daquer, E.M.A., Paiva, M., Zahn, R., Grafman, J., 2007. The self as a moral agent: Link-ling the neural bases of social agency and moral sensitivity. Social Neuroscience 2, 336-352.

Moll, J., Eslinger, P.J., de Oliveira-Souza, R., 2001. Frontopolar and anterior temporal cortex activation in a moral judgment task - Preliminary functional MRI results in normal subjects. Arquivos De Neuro-Psiquiatria 59, 657-664.

Nelissen, R.M.A., Dijker, A.J.M., de Vries, N.K., 2007. How to turn a hawk into a dove and vice versa: interactions between emotions and goals in a give-some dilemma game. Journal of Experimental Social Psychology 43, 280-286.

Oldfield, R.C., 1971. Assessment and Analysis of Handedness - Edinburgh Inventory. Neuropsychologia 9, 97-113.

Rilling, J.K., Gutman, D.A., Zeh, T.R., Pagnoni, G., Berns, G.S., Kilts, C.D., 2002. A neural basis for social cooperation. Neuron 35, 395-405.

Rilling, J.K., Sanfey, A.G., Aronson, J.A., Nystrom, L.E., Cohen, J.D., 2004. Opposing BOLD responses to reciprocated and unreciprocated altruism in putative reward pathways. Neuroreport 15, 2539-2543.

Sanfey, A.G., Rilling, J.K., Aronson, J.A., Nystrom, L.E., Cohen, J.D., 2003. The neural basis of economic decision-making in the ultimatum game. Science 300, 1755-1758.

Schultz, W., Tremblay, L., Hollerman, J.R., 2003. Changes in behavioral-related neuronal activity in the striatum during learning. Trends in Neuroscience 26, 321-328.

Simpson, B., 2004. Social values, subjective transformations, and cooperation in social dilemmas. Social Psychology Quarterly 67, 385-395.

Spitzer, M., Fischbacher, U., Herrnberger, B., Gron, G., Fehr, E., 2007. The neural signature of social norm compliance. Neuron 56, 185-196.

Stuss, D.T., Levine, B., 2002. Adult clinical neuropsychology: Lessons from studies of the frontal lobes. Annual Review of Psychology 53, 401-433.

Talairach, J., Tournoux, P., Musolino, A., 1988. Anatomical Stereotaxic Studies of the Frontal-Lobe in the Management of the Epilepsies. Epilepsia 29, 205-205.

Tricomi, E.M., Delgado, M.R., Fiez, J.A., 2004. Modulation of caudate activity by action contingency. Neuron 41, 281-292.

Tulving, E., 1985. Memory and Consciousness. Canadian Psychology-Psychologie Canadienne 26, 1-12.

Van Lange, P.A.M., 2000. Beyond self-interest: A set of propositions relevant to interpersonal orientations. In: Stroebe, W., Hewstone, M. (Eds.), European Review of Social Psychology. Wiley, New York, pp. 297-331.

Van Opstal, F., Verguts, T., Orban, G.A., Fias, W., 2008. A hippocampal - parietal network for learning an ordered sequence. NeuroImage 40, 333-341.

Walter, H., Abler, B., Ciaramidaro, A., Erk, S., 2005. Motivating forces of human actions - Neuroimaging reward and social interaction. Brain Research Bulletin 67, 368-381.

Winston, J.S., Strange, B.A., O'Doherty, J., Dolan, R.J., 2002. Automatic and intentional brain responses during evaluation of trustworthiness of faces. Nature Neuroscience 5, 277-283.

Wright, P., Albarracin, D., Brown, R.D., Li, H., He, G.J., Liu, Y.J., 2008. Dissociated responses in the amygdala and orbitofrontal cortex to bottom-up and top-down components of emotional evaluation. NeuroImage 39, 894-902.