

Comparing the Neural Basis of Decision Making in Social Dilemmas of People With Different Social Value Orientations, a fMRI Study

Griet Emonds, Carolyn H. Declerck, and
Christophe Boone
University of Antwerp

Everhard J. M. Vandervliet and
Paul M. Parizel
University of Antwerp and Antwerp University
Hospital (UZA)

Using functional MRI, we investigate the neural correlates of intrinsic versus extrinsic motivation to cooperate by comparing people who differ in the personality trait Social Value Orientation. Participants ($n = 28$) played several one-shot prisoner's dilemma games (offering weak cooperative incentives) and coordination games (offering strong cooperative incentives) with anonymous partners while they were under the scanner. Behavioral results indicate that prosocial individuals adjust their behavior toward more cooperation when extrinsic incentives were present, while prosocials' decisions are not affected by game context. The neurological data is consistent with a priori developed hypotheses regarding different behavioral strategies, and suggest that extrinsically motivated prosocial strategies are driven by calculation and a situation-by-situation approach. Increased activation was found in dorsolateral prefrontal cortex, posterior superior temporal sulcus (STS), and precuneus. Intrinsically motivated prosocials' strategies reflect norm compliance, routine moral judgment, and social awareness. Increased activation was found in lateral orbitofrontal cortex, anterior STS, and inferior parietal lobule.

Keywords: social dilemma, fMRI, social value orientation, cooperation

Much experimental research in different scientific domains has been devoted to understanding the strategies people use in social interactions. Often, these interactions are interdependent, meaning that the outcome is uncertain because it is determined by the combination of strategies of all interacting partners. Understanding how cooperative decisions particularly are made under uncertainty has been approached from different angles. Behavioral economists are increasingly stressing the impor-

tance of heterogeneity of social preferences in determining the aggregate outcome of social interactions (Camerer & Fehr, 2006). Social psychologists have long 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 & 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 & McClintock, 1968), it can be considered an important determinant of cooperative motives, strategies, and choice behavior (Kollock, 1998; McClintock & Van Avermaet, 1982). Much research (reviewed in Bogaert, Boone, & Declerck, 2008) 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

This article was published Online First November 8, 2010.
Griet Emonds, Carolyn H. Declerck, and Christophe Boone, Faculty of Applied Economics, University of Antwerp; Everhard J. M. Vandervliet and Paul M. Parizel, Faculty of Medicine, University of Antwerp, and Antwerp University Hospital (UZA).

We thank Armin Heinecke and Prof Wim Fias for their assistance regarding data analysis. This study was funded by ID BOF 1931 from the University of Antwerp.

Correspondence concerning this article should be addressed to Griet Emonds, University of Antwerp, Faculty of Applied Economics, Prinsstraat 13, 2000 Antwerpen, Belgium. E-mail: griet.emonds@ua.ac.be

a “dove strategy,” opting for the 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 reap the benefits for themselves. The experimental research that has substantiated these differences between prosocials and proselfs was often carried out in game-theoretic settings. This has revealed that prosocials are more likely to cooperate by default in the well-known prisoner’s dilemma game,¹ while proselfs typically defect (Bogaert, Boone, & Declerck, 2008). However, proselfs can still be induced to cooperate when there are extrinsic incentives that make cooperation rewarding, as is the case in a coordination game (also known as the assurance game, Stag Hunt, or trust dilemma).² Several authors have suggested that only proselfs adapt their behavior toward more cooperation in the coordination game (CG) and more defection in a prisoner’s dilemma (PD), while prosocials play a prisoner’s dilemma as if it were a coordination game, maintaining a high level of cooperation in both games. They naturally transform the PD pay-off matrix to a CG pay-off matrix (Acevedo & Krueger, 2005; Simpson, 2004). In fact, this was recently tested and corroborated in a series of laboratory experiments (Boone, Declerck, & Kiyonari, work in progress). These authors investigated 322 participants³ (48% prosocials and 52% proselfs) playing both a one-shot PD and CG game with a real interaction partner and for real money. The order of PD and CG was counterbalanced across participants. Prosocials were found to cooperate significantly more in both games compared to proselfs. While both prosocials and proselfs cooperated more in the CG than the PD, the proselfs showed a much greater increase in cooperation levels (for prosocials [$n = 156$]: 48% cooperation in PD and 66% in CG, $\chi^2 = 9.55$, $p < .002$; for proselfs [$n = 166$], 20% cooperation in PD and 52% in CG, $\chi^2 = 36.8$, $p < .002$).

To complement the abundance of behavioral research on cooperation in social dilemmas (e.g., the PD), researchers are beginning to unravel the neural correlates of social decision making (e.g., Rilling et al., 2008; Rilling et al., 2002; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004a, 2004b). However, few studies have looked at the impact of individual differences in personality on brain activation during

social decision making (but see Rilling et al., 2007; Spitzer, Fischbacher, Herrnberger, Gron, & Fehr, 2007, for exceptions). To better understand the nature of cooperative decision making in social interactions, we believe that a comparative approach analyzing how the brains of individuals with opposing intrinsic social motives process alternative extrinsic incentive structures might be revealing. Therefore, in this study we investigate the effect of the personality trait SVO on social decision making in interdependent, uncertain situations. Because we know that people with different social value orientations are differentially affected by extrinsic incentives, we compare the neural correlates of decision making for prosocials and proselfs while they are playing the two economic games mentioned earlier: the PD with weak cooperative incentives, and the CG with strong cooperative incentives. A major aim of this study is to investigate whether there are neural differences between prosocials and proselfs that can account for the different strategies they use when solving a social dilemma. We hope to substantiate with fMRI that prosocials approach a social dilemma with intrinsic motivation (implying no difference in cooperation between PD and CG), while proselfs approach a dilemma with extrinsic motivation (leading them to cooperate in CG and defect in PD).

Based on current knowledge of social dilemmas and the growing literature on the neural basis of intrinsic and extrinsic motivators during social and strategic decision making, we

¹ The prisoner’s dilemma game is an economic game with weak cooperative incentives, as it naturally provides a temptation to free-ride on other’s cooperation, but at the risk of losing potential gains from a mutually beneficial relationship. 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.

² In contrast to the prisoner’s dilemma game, the structure of a coordination game holds strong cooperative incentives, as the payoff from defection is reduced to or below the level of the payoff from mutual cooperation. While decision making still yields an uncertain outcome, the conflicting 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 coordination compared to prisoner’s dilemma games (Kollock, 1998).

³ These data were obtained during three separate experiments, the results of which are to be published elsewhere.

have developed specific hypotheses with regards to how brain activation might differ for people with a prosocial versus a proself orientation confronted with a social dilemma.

With respect to proselfs, we expect that their calculative strategies, needed to adapt their behavior according to the highest payoff, correspond with increased activity in the dorsolateral prefrontal cortex (DLPFC). The DLPFC is typically active during tasks requiring increased cognitive control and working memory (Carter & van Veen, 2007; Krueger, Grafman, & McCabe, 2008; E. K. Miller & Cohen, 2001; Rilling et al., 2007; Weissman, Perkins, & Woldorff, 2008). "Rational" decision making in strategic, economic games was previously shown to correlate with superior working memory (Devetag & Warglien, 2003).

With respect to prosocials, we expect increased activation in regions of the temporoparietal junction that has previously been implicated in moral or prosocial decision making. Prosocials approach social dilemmas first and foremost with social responsiveness, whereby they aspire an equal outcome for themselves and their partner. Compared to proselfs, prosocials are more concerned about the outcome for others (Van Lange, 2000), and they also tend to be more empathic (Declerck & Bogaert, 2008). However, prosocials are not unconditionally altruistic; they are behavioral assimilators who stop cooperating when they expect that it will not be reciprocated (Bogaert, Boone, & Declerck, 2008; Fehr, Fischbacher, & Kosfeld, 2005; Simpson, 2004). Accordingly, they tend to have superior mentalizing skills to assess trustworthiness and avoid betrayal (Declerck & Bogaert, 2008). Therefore, we expect that the decision making style of prosocials will be characterized by both perspective taking and morality. Many studies that attempt to locate the neural correlates of perspective-taking, theory of mind, empathy, and moral judgment, have pointed to the role of the superior temporal sulcus (STS) (e.g., Borg, Hynes, Van Horn, Grafton, & Sinnott-Armstrong, 2006; C. D. Frith & Frith, 2006; U. Frith & Frith, 2001; U. Frith & Frith, 2003; Fukui et al., 2006; Greene & Haidt, 2002; Moll et al., 2007) and the inferior parietal lobule (IPL) (see, e.g., Borg, Hynes, Van Horn, Grafton, & Sinnott-Armstrong, 2006; Decety, Jackson, Sommerville, Chaminade, & Meltzoff, 2004; C. D. Frith &

Frith, 2006; Greene & Haidt, 2002). The STS region is involved in complex social behavior, and was found to be particularly important with respect to the ability to predict the next move in a behavior sequence, an ability that is extremely important in social exchanges (Fukui et al., 2006). The STS is further described by Frith and Frith (2003) as part of the mentalizing system. Consistent with this, Rilling et al. (2004a) found STS to be significantly more activated when people played a PD game and an Ultimatum game against another person (the social condition) compared to when they played the same games against a computer (the asocial condition). The IPL is specifically implicated in distinguishing between actions by self and others (Decety et al., 2004), and in moral judgments that involve unintentional versus intentional harm (Greene & Haidt, 2002; Moll et al., 2007). We expect the STS/IPL regions to be more active for intrinsically cooperative prosocials because for them, cooperation is a moral decision which requires coordination between their own behavior and the behavior of others to reach a mutually desired outcome. Proselfs, on the other hand, care less about the social or moral aspect of the interaction as they tend to focus solely on their own outcome.

Additionally, we expect prosocials to show increased activation in regions associated with norm-compliance when involved in a social exchange, as they are believed to have internalized social norms associated with cooperation and social responsibility (De Cremer & Van Lange, 2001). A study by Spitzer et al. (2007) specifically associated norm compliance with increased activity in the lateral orbitofrontal cortex. Activation in this region is thought to prevent engaging in inappropriate, norm transgressing behavior (Berthoz, Armony, Blair, & Dolan, 2002). Similarly, Kringelbach and Rolls (2004) report that damage to the lateral regions of the orbitofrontal cortex early in life results in behavioral conduct problems that remain insensitive to corrective or normative influences.

A recent study by Li et al. (2009), is particularly relevant with respect to the hypotheses we have formulated. These authors set out to investigate with fMRI why introducing sanctions in social interactions tends to have a detrimental effect on reciprocity. They hypothesize that the presence of sanctions tends to crowd out

the intrinsic motivation to be cooperative by causing a perceptual shift from socially motivated decision making to cognitive decision making. Without sanctions, reciprocators in a trust game are expected to engage in intrinsically motivated, norm-sensitive decisions. However, the presence of sanctions leads to calculative and utility-based decision making. The results of the study show that norm-sensitive decisions (reciprocating in an interaction without sanctions) are associated with increased activity in the lateral orbitofrontal cortex, while utility-based decisions (reciprocating when sanctions are present) are associated with increased activity in the DLPFC. We believe that the norm-sensitive decisions (in the no-sanction condition) correspond to the intrinsic cooperative motivation of prosocials, while the utility-based decisions (in the sanction condition) correspond to the extrinsic cooperative motivation of proselves. In the study by Li et al. (2009), DLPFC BOLD signals correlated negatively with the individual's willingness to cooperate (conceptualized as the ratio of actual vs. maximum possible back payment), and hence capture the Nash strategy in this trust game (Li et al., 2009).

To summarize, in this study we expect to find that proselves show more activity in the DLPFC (being more calculative and strategic). Prosocials, on the other hand, being more inclined toward morality and the perspective of others, and being more norm compliant, are expected to show more activity in the STS, IPL, and in the lateral orbitofrontal cortex. Additionally, we will also explore whether the contrast between prosocials and proselves is moderated by the type of game.

Materials and Method

Experimental Design

The study was conducted in a blocked design with 3 different conditions, each one separated by a brief rest: a prisoner's dilemma, coordination, and control condition. The two games make up the within-subject factor of our 2×2 factorial design.⁴ The between-subjects factor consists of the prosel self or prosocial orientation of the participants.

The two games were explained to participants as one single "investment game" (without

differentiating between the prisoner's dilemma and the coordination 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. Figure 1a and 1b represent two possible decision pay-off matrices as shown under the scanner. Rows correspond to the decision of the participant (denoted "I"), and columns correspond to the decision of the other player (denoted by "person x"). The numbers in each of the four boxes represent the participant's pay-off for the combination of choices made by him or herself and the other person. The pay-off for the other person is shown in parentheses. In the coordination game (Figure 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 prisoner's dilemma game (Figure 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 or she is afraid of betrayal. From an economic viewpoint, "not investing" is the dominant response (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. 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 condition⁵ 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.

⁴ The investigation of how the neural basis of social decision making in interdependent situations differs in the presence of weak (PD) versus strong (CG) extrinsic incentives will be discussed in a separate paper.

⁵ 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.

a			b		
Person 18			Person 15		
	Invests	Does not invest		Invests	Does not invest
Invest 	2 (2)	0 (1)	Invest 	2 (2)	0 (3)
Do not invest	1 (0)	1 (1)	Do not invest	3 (0)	1 (1)

Figure 1. Examples of each of the two game conditions used in the design as shown to the subjects inside the scanner. Numbers in parentheses are points earned by the other player for each possible outcome. The image of the bell reminds participants for which choice they should push the button and for which they should not. The number above the matrix corresponds to the partner with which the participant is coupled for this specific interaction. (a) Coordination Game (b) Prisoner's Dilemma Game.

Each block lasted for 30 s, during which 4 different matrices with the same game structure (prisoner's dilemma or coordination game) were shown (or 5 different numbers for the control condition). There were 7 cycles in which blocks of all three conditions were randomly alternated. Each block was always followed by a 30 s resting period. The total scanning time for acquiring the functional data was 21 min.

Participants

Participants ($n = 28$) were recruited at the University of Antwerp through e-mail and Web-based announcements. Monetary incentives were emphasized. All right-handed candidates⁶ 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. Upon completing the task, participants can be classified 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 individu-

alistic orientation. We refer to the latter as the "proself" orientation, which differs slightly from conventional nomenclature where the individualistic and the competitive orientations are often combined and called prosself.

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). None of the participants had a history of neurological or psychiatric illness, were on any medication, or suffered from claustrophobia. All candidates signed an informed consent form before participating. Above procedures were approved by the Commission of Medical Ethics at the University of Antwerp.

Behavioral data were obtained for all participants, but the data of two participants were excluded from the behavioral analysis because of a possible error in recording. The behavioral data analysis thus included data from 26 participants (14 prosocials and 12 proselfs, 13 men and 13 women, mean age = 25 years, ranging from 19 to 33 years). Because of technical problems with the scanner, the fMRI images of 4 participants were not measured correctly and

⁶ Candidates who indicated that they were ambivalent about their handedness were asked to fill in a questionnaire (translated and adapted from Oldfield, 1971). Based on this assessment, one candidate was still allowed to participate in the study.

these subjects therefore had to be excluded from the fMRI data analysis. One subject showed unusually large ventricles, and this fMRI dataset was therefore also excluded. Eventually, 23 participants (12 prosocials and 11 proselves) were included for the fMRI data analysis (13 men and 10 women, mean age = 24.1 year, ranging from 19 to 33 years).

Procedures

Participants 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 Figure 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.

Participants were told that they would not receive any feedback during the course of the scanning session. After each trial, their decision would be matched with that of their partner for that trial, but the joint outcome would not be revealed. At the end of the experiment they would receive the amount of money corresponding to the cumulative outcome of all the interactions. Even if we emphasized that each trial was a single interaction with a particular individual, feedback might have still inadvertently influenced the participant's decision on the next trial. Therefore, we opted for a design consisting of a series of one-shot interactions with no feedback.

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% cooperation and 50% defection).

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 control 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.

For debriefing purposes, participants were later contacted by mail and referred to a website where the intent, results, and procedures of the experiment in which they had participated were fully 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 20.59 Euro and did not differ between the prosocial and the prosself groups.

After completing the fMRI experiment, subjects filled in a translated and adapted version of the General level of trust questionnaire from

Yamagishi et al. (1986). The test comprises 6 questions that are scored on a 7-point Likert scale. Cronbach α for this scale was 0.741.

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 (256×256 matrix, 176 1 mm sagittal slices, FOV = 256 mm). During the same session, functional images were acquired using T_2^* -weighted EPI (TR = 3,000 ms, TE = 50 ms, 384×384 image resolution, FOV = 192 mm, 35 4 mm slices without gap, voxel size = $3 \times 3 \times 4$ mm).

Data Analysis

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 $3 \times 3 \times 3$ mm configuration. For spatial normalization of the images, the standard 9 parameter landmark method of Talairach and Tournoux, implemented in BrainVoyager, was used (Talairach, Tournoux, & Musolino, 1988).

For each participant, a general linear model (GLM) was created with the percent BOLD signal change as dependent variable, and with 9 regressors: the prisoner's dilemma, coordination and control conditions, 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, the effects of two regression coefficients of interest, the PD and CG conditions, were combined and one-sample t tests were performed contrasting the prosself group with the prosocial group ($(PD + CG)_{\text{prosselfs}} - (PD + CG)_{\text{prosocials}}$).

The whole-brain statistical map was corrected for multiple comparisons using cluster

size thresholding. The initial voxel-level (uncorrected) threshold was set at $p < .005$. 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 1,000 iterations (Monte Carlo simulation) for estimating cluster-level false-positive rates, a minimum cluster-size threshold of 135 anatomical voxels, that yields a cluster-level false-positive rate of 5%, was applied to the statistical maps (Forman et al., 1995; Goebel, Esposito, & Formisano, 2006).

For the main contrast between proselves 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 procedures of studies by Li et al. (2009), Van Opstal et al. (2008), and Wright et al. (2008) and removed the cluster threshold, accepting contrast values as significantly different from zero when $p < .005$. To verify 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 reflects a main effect of SVO.

In the whole brain analysis, we noted a large cluster of activation (122 voxels) in the precuneus, a region that has regularly been implicated in social cognition and self-referencing tasks (Cavanna & Trimble, 2006). Because these functions may be important with respect to the SVO construct, we include this cluster in subsequent ROI analyses.

Results

Behavioral Data

Our behavioral results are illustrated in Figure 2. We analyzed the data in panel form ($n = 26$ individuals $\times$ 56 decisions) using binary logistic regressions with robust standard errors. Cooperative behavior is regressed on SVO and game type (cooperative behavior = 1, prosocial = 1, coordination game = 1, 0 otherwise), controlling for different payoff matrices. First, consistent with previously published results, the behavioral data obtained from our sample

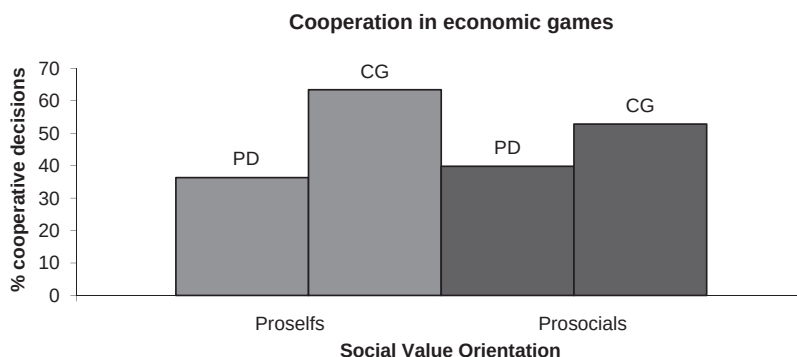


Figure 2. Percentage of cooperative decisions made by proselves and prosocials in PD and CG. Overall there is more cooperation in the CG ($Z = 4.63$ with $p < .001$). We additionally found an interaction effect between SVO and type of game showing that proselves (but not prosocials) cooperate more in CG compared to PD ($Z = -1.56$ with $p = .056$). The main effect of SVO did not reach significance. PD = Prisoner's Dilemma; CG = Coordination Game.

showed more cooperation in the coordination than in the prisoner's dilemma game ($\beta = 0.8362$; $p < .00$, one-tailed) (e.g., Erev, Bornstein, & Galili, 1993; Harrison & Hirshleifer, 1989; Kiyonari, Tanida, & Yamagishi, 2000; Simpson, 2004). Second, unlike expected, prosocials did not show significantly more overall cooperation compared to proselves. While the small sample size makes it difficult to reach statistical significance, there may also be an underlying reason for the relatively low cooperation rate of prosocials in this particular study. As explained in the introduction, prosocials' intrinsic motivation to cooperate is conditional on trust and their expectations that their cooperative acts will be reciprocated (Bogaert, Boone, & Declerck, 2008). This particular laboratory setting, having to solve social dilemmas in a clinical environment and inside an MRI scanner, might have had reverse effects on prosocials' general trust that in turn could interfere with their intrinsic cooperative motivation. Therefore, we tested if the cooperative decisions of prosocials were moderated by their general level of trust. Indeed, the interaction between SVO and general trust reaches significance ($\beta = 0.5662$; $p = .07$, one-tailed), indicating that prosocials with greater trust are more cooperative. This result is consistent with the study of Boone, Declerck, and Kiyonari (2010, $N = 322$) indicating that prosocials' cooperative behavior is strongly affected by both their generalized level of trust and experimentally

induced trust.⁷ Finally, as expected, proselves adapt their behavior more according to game type: we found an interaction effect between SVO and type of game, showing that proselves (but not prosocials) cooperate more in the coordination game compared to the prisoner's dilemma ($\beta = -0.5566$; $p = .056$, one-tailed).

fMRI Data

For the contrast between prosocials and proselves, the hypotheses that we developed in the introduction were specifically tested. As predicted, the whole brain analysis (without multiple comparisons corrections [see also Van Opstal, Verguts, Orban, & Fias, 2008; Wright et al., 2008]) reveals more activation for proselves in the DLPFC, more specifically in BA 9. Unlike predicted, proselves also show more activation in the temporo-parietal junction (BA 39) and in the precuneus. Among prosocials there is also more activation at the temporo-parietal junction, more specifically in the anterior STS (BA 22) and IPL (BA 40). We also find more

⁷ An alternative hypothesis was presented by one of the reviewers, suggesting that prosocials might cooperate less because they stop cooperating because of the lack of (cooperative) feedback. To test this, we investigated whether there was an interaction effect between SVO and trial number on cooperation. This was not the case. The level of cooperation did not decline more along the course of the experiment for prosocials than for proselves. Neither did prosocials cooperate more in the first round of PD games.

activation of the lateral orbitofrontal cortex (BA 10) in prosocials. The results of this analysis are shown in the left side of Table 1.

The ROI analysis (right side of Table 1) corroborates the whole-brain analysis and thus indicates that the detected clusters are all clusters likely to be regions of 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 ROIs, however, showed a significant interaction effect. We acknowledge that this procedure has recently been challenged by some fMRI researchers because the data on which both analyses are based are not independent. Kriegeskorte et al. (2009) describe how such selective analysis may distort the results because of noise in the data. Specifically, “overfitting” an ROI occurs when voxels at the fringe of a cluster are incorrectly included. By simulating a block-design fMRI experiment at $p < .01$, the authors found that the distortion lead to spurious statistically significant results for ROI contrasts 9 out of 100 times. Kriegeskorte et al. further report that the magnitude of possible distortions depends on many factors. Especially complex models including many parameters, testing linear classifiers rather than contrasting ROIs, and high resolution fMRI, cause the data

to be prone to overfitting. Constraints regularizing the data selection, such as spatial smoothing, reducing the number of selection channels, and the spatial contiguity of the voxels of interest, on the other hand, can reduce a model’s effective complexity and reduce the distortion. Thus, while our design made use of nonindependent selective analysis, we believe we limited the distortion effect by the fact that we tested a simple model (2 parameters) at $p < .005$, that we contrasted contiguous ROIs, that we spatially smoothed the data during our pre-processing procedures, and that we collected the data with a small number (8) of channels.

Discussion

The aim of our study was to understand how the brains of individuals with different social orientations respond to social exchanges under uncertainty. To accomplish this, an fMRI study was performed to test specific hypotheses. We investigated which brain regions were active when individuals with opposing cooperative motives played two economic games: a prisoner’s dilemma and a coordination game. With this, we hoped to identify fundamental neural differences between people with a prosocial versus a prosself social value orientation that

Table 1

Main Effect of Social Value Orientation on Decision Making in Social Dilemmas (Proselfs vs. Prosocials)

Region	BA	Side	X	Y	Z	Size	$t_{(21)}$	ROI analysis (Pse-Pso)	
								$t_{(21)}$	p
Frontal lobe									
Superior frontal gyrus	9	L	−8	57	31	22	3.800	3.960	<0.001
	10	R	27	60	2	16	−3.805	−3.338	0.003
Temporal lobe									
Superior temporal gyrus	22	L	−56	3	−2	34	−4.281	−2.951	0.007
		R	48	2	−2	10	−3.589	−3.833	<0.001
Parietal lobe									
Inferior parietal lobule	40	L	−52	−34	31	62	−3.662	−4.018	<0.001
Angular gyrus	39	R	52	−60	31	5	3.318	3.243	0.004
Precuneus	7	R	4	−57	41	122	3.650	3.309	0.003

Note. Left side of table: A priori defined regions for which differences between prosocials (Pso) and prosselfs (Pse) 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, $p < .005$). Right side of the table: ROI analysis (see text for details). $t_{(21)}$ = t values from student t test with 21 df ; Positive t values refer to more activation in prosselfs compared to prosocials, negative t values refer to more activation in prosocials than prosselfs; p = p value; BA = Brodmann Area; L = Left; R = Right; X, Y, Z = Talairach coordinates of mean voxel of cluster; size = number of 1 mm³ voxels; SVO = social value orientation. Scores from whole-brain analysis are taken from the peak voxel of the cluster; scores from ROI analysis represent the mean for each cluster.

could account for their different strategies in social interactions.

Our behavioral and fMRI results are in line with our expectations regarding the influence of individual differences in SVO on cooperation. Our behavioral data was consistent with recent findings on SVO indicating that the *difference* in cooperative decision making between the prisoner's dilemma and the coordination game is especially pronounced for individuals with a prosself orientation (Boone, Declerck, & Kiyonari, work in progress). This fundamental behavioral difference lead us to hypothesize that proselves are strategizers, calculating maximum pay-offs for each game, while prosocials are norm complying and approach each game with a moral consideration of the outcome for others. We performed ROI analyses on a priori defined brain regions to look for support of these hypotheses.

For proselves, we found clusters of increased activation (compared to prosocials) in the DLPFC (BA 9), a region that has previously been associated with conceptual and calculative reasoning processes, mentalizing about the self, and rational decision making (Fukui et al., 2006; E. K. Miller & Cohen, 2001; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003; Stuss & Levine, 2002; Weissman, Perkins, & Woldorff, 2008). This result supports the view that proselves are especially interested in positive

outcomes for themselves, and that they approach the games in a calculative and strategic manner. An additional ROI was found to be more activated in the proselves in the temporo-parietal junction (BA 39) touching on the posterior STS (see right panel of Figure 3), a region that is often implicated in perspective taking (Fukui et al., 2006). Although this was not the direction in which we expected STS to be activated, it is, in retrospect, not surprising that perspective taking would be important to proselves as well. After all, it is because proselves understand the point of view of the other player that they realize that a coordination game yields a cooperative advantage. The insight that the other player irrevocably benefits from cooperation in a coordination game prompts proselves to cooperate more in this game.

An unexpectedly large cluster of activation in the precuneus was also observed for prosself individuals. This finding too is in retrospect not too surprising, considering what is so far known about this structure. Cavanna and Trimble have reviewed the functional anatomy and behavioral correlates of the precuneus, and conclude that it contributes significantly to a variety of higher order cognitive functions. Especially the anterior portion of the precuneus (where we find the cluster of activation) has been implicated in social cognition tasks differentiating between a

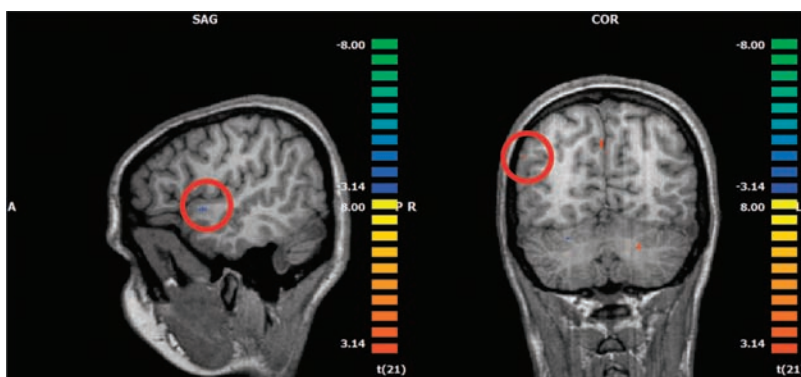


Figure 3. Significant clusters of activation in whole-brain random effects analysis contrasting proselves and prosocials (Pse-Pso) after removing cluster size threshold ($p < .005$). Color bar denotes t values. Left: the contrast showed more activity in the right anterior superior temporal sulcus (STS) (BA 22) in prosocials than proselves (encircled) (sliced at $x = 48$). Right: touching on the right posterior STS (BA 39) there was more activity in the prosself group compared to the prosocials (encircled) (sliced at $y = -61$). $t_{(21)}$ = t values from student t test with 21 df ; Sag = Sagittal view; Cor = Coronal view; A = Anterior; P = Posterior; L = Left; R = Right.

first and third person perspective (Cavanna & Trimble, 2006). Especially interesting are studies that show that the precuneus is more activated when processing self-relevant (compared to irrelevant) information (Kircher et al., 2000), and that it is specifically involved in processing intentions that are related to the self (den Ouden, Frith, Frith, & Blakemore, 2005). Therefore, our results suggest that proselves may show more precuneus activity when solving a social dilemma because they intentionally weigh the outcome of their decision with reference to what is best for themselves.

For prosocials, our hypothesis regarding norm compliance was confirmed by clusters of activation in the lateral OFC. This region has been associated with the subjective representation of punishment, as well as with norm compliance (Berthoz, Armony, Blair, & Dolan, 2002; Kringelbach & Rolls, 2004; Spitzer, Fischbacher, Herrnberger, Gron, & Fehr, 2007). Spitzer et al. (2007) also found greater activation of the lateral OFC in a social economic game when players were complying to a cooperative norm because of a punishment threat. This is consistent with behavioral data suggesting that for prosocials, norm compliance and/or the threat of social punishment (guilt or shame), are automatic, internalized processes that surface during decision making in social interaction (Nelissen, Dijk, & de Vries, 2007).

As predicted, clusters of increased activation in prosocials were further found in the IPL (BA 40) and the STS (BA 22). The finding that the IPL (BA 40) is more activated in prosocials compared to proselves may reflect their greater moral awareness during decision making. Like Walter et al. (2005), Borg et al. (2006) associate BA 40 with the ability to evaluate one's sense of agency with a sense of moral responsibility. The STS is commonly considered to be part of the mentalizing and perspective taking network (e.g., Borg et al., 2006; Decety, Jackson, Sommerville, Chaminade, & Meltzoff, 2004; U. Frith & Frith, 2003; Fukui et al., 2006; Greene & Haidt, 2002; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004a). Fukui et al. (2006) associate this region with "higher cognitive functions needed in social interaction."

The unexpected finding that different regions of the STS are activated in prosocials compared to proselves is particularly interesting considering recent reports on the functional differentiation of the

STS (Borg et al., 2006, p. 811). In our study, only the anterior STS was more activated in prosocials, while the posterior STS was in fact more activated in proselves (activation patterns of both anterior and posterior STS are illustrated in Figure 3). This is consistent with Borg et al.'s notion that "the posterior STS may play a preferential role in thought-provoking first time moral judgment that requires executive resources, whereas the anterior STS may be more involved in previously resolved routine moral judgment that requires more semantically based representational knowledge." This differentiation between posterior and anterior STS is consistent with the strategies we have so far described for proselves and prosocials. Proselfs use more cognitive, calculative strategies to solve any dilemma, and they decide by figuring out "hic und nunc" incentive structures. 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 external incentives. Their decision making strategy is characterized by routine moral judgment, which is reflected in their pattern of STS activation.

The fact that the proself-prosocial contrasts did not depend on the type of game (no significant interaction effects in our fMRI data) underscores that people with different intrinsic motives approach social interactions in fundamentally different ways. When confronted with a social dilemma, the incentive structure does not alter the underlying neural network during decision making. We believe that a substantial contribution of this work therefore consists of confirming that there does not necessarily have to be a one to one relationship between brain activity and attitude or behavior (G. Miller, 2008). The finding that prosocials activate parts of "the moral brain" (IPL, STS) when they are confronted with a social dilemma situation, does not necessarily mean that they will actually cooperate more in that situation. The activation of these parts of the brain merely indicates that the perception of social interaction has a different connotation to them compared to proselves. Their actual cooperative decision will further be moderated by other inputs, such as their assessment of trust signals. Likewise, the activation of calculative regions in the brains of proselves when they are confronted with a social dilemma does not necessarily mean they will always defect. In fact, the cognitive control associated

with DLPFC has been suggested to be one of the requirements in the evolution of cooperation (Stevens & Hauser, 2004). This is consistent with our behavioral data, which shows that proselves did cooperate as much as prosocials in the current experiment (in part because of proselves' high cooperation rate in the CG that provides explicit cooperative incentives). The one conclusion we can draw is that proselves use a more calculative way of processing information that is relevant during social exchanges. We infer that DLPFC is activated to process the presence or absence of external incentives.

Our interpretation of the data is compatible with other fMRI research on individual differences in emotion processing, indicating that similar stimuli may evoke different neural responses in people with different personalities (Canli et al., 2001; Hutcherson, Goldin, Ramel, McRae, & Gross, 2008). Furthermore, similar behavioral responses may also be associated with different neural responses, depending on personality. For example, people scoring high or low on psychopathy tend to have reversed patterns of activity in the DLPFC and OFC when making cooperative or defect decisions (Rilling et al., 2007).

A major limitation of this study, however, is that we identify ROI based on the results of a whole brain analysis of the same dataset. Therefore, we acknowledge that the data we present need to be interpreted with caution. However, as our findings underscore what is so far known about the link between brain and behavior for different decision making strategies, we believe this study forms a good starting point for further investigation. Future studies that look into the neural differences accounting for different behavioral strategies of prosocials and proselves may eventually confirm or amend the current findings. Another limitation is that we have only addressed a fraction of possible a priori hypotheses, and there may be numerous other differences between prosocials and proselves that we did not consider in our ROI's. Finally, because we preferred to use a block design for addressing fundamental differences between two personality types, we cannot draw any conclusions about actual cooperative decisions. Future research could investigate how the neural correlates of cooperative (vs. defect) decision making differ for proselves versus prosocials.

Conclusion

In conclusion, the imaging data presented in our study suggest that people with opposing social motives ("hawks" and "doves") may rely on fundamentally different strategies to solve problems related to social exchanges, as their brains show different patterns of activation. Individual differences in social value orientation appear to be an additional influence on the decision making process in prisoner's dilemma and coordination games. Proselfs are especially concerned with their own outcome and approach the games in a calculative manner (activating the precuneus and the DLPFC, respectively). Relying on such a "hawk" strategy, they are very sensitive to the presence of either external incentives or mixed motives, and calculate how to best adapt their behavior according to the game structure. In this experiment proselves indeed adjusted their decisions according to the game type. Prosocials, on the other hand, perceive both games as similar social interactions in which each time a mutually beneficial outcome is their most desirable option. Consistent with other fMRI reports on social interactions and moral judgments, this appears to activate the IPL and STS. Furthermore, their decision making style appears more norm compliant (activating lateral OFC). People with such a "dove" strategy approach social exchange situations with a strong emphasis on their internalized norms that surface during social interaction and with much less attention for external incentives. This explains prosocials' typical behavioral pattern, showing little or no difference between decisions in a mixed motive versus a coordination game.

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