

The Neural Bases of Framing Effects in Social Dilemmas

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Human behavior in social dilemmas is strongly framed by the social context, but the mechanisms underlying this framing effect remain poorly understood. To identify the behavioral and neural responses mediating framing of social interactions, participants underwent functional MRI while playing a prisoner's dilemma game. In separate neuroimaging sessions, the game was either framed as a cooperation game or a competition game. The framing of social decisions engaged the hippocampal formation, precuneus, dorsomedial prefrontal cortex, and lateral temporal gyrus. Among these regions, the engagement of the left hippocampus was further modulated by individual differences in empathy. Social decisions not adhering to the frame were associated with stronger engagement of the angular gyrus and trend increases in lateral orbitofrontal cortex, posterior intraparietal cortex, and temporopolar cortex. Our findings provide the first insight into the mechanisms underlying framing of behavior in social dilemmas, indicating increased engagement of the hippocampus and neocortical areas involved in memory, social reasoning, and mentalizing when participants make decisions that conform to the imposed social frame.

Keywords: social reasoning, prisoner's dilemma, fMRI, framing, mentalizing

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Social interaction between humans often constitutes a dilemma. Although in many situations cooperation between two or more agents leads to increased benefits for everyone, the individual often can benefit more from selfish behavior rather

than from mutual cooperation. The propensity to put oneself first takes into account how one's own selfish actions may trigger sanctions by the interaction partner (Fehr & Gintis, 2007; Fehr & Schmidt, 1999). Further, one may first exploit the

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cooperative behavior of the other group members before engaging in cooperative interactions (Baumgartner, Fischbacher, Feierabend, Lutz, & Fehr, 2009). In other words, when engaging in social interactions, one's self-interest is weighted against the concerns for the intentions and behavior of others and how the interaction partners may respond to one's actions.

The factors that drive decisions in such social dilemmas have been studied in economic and psychological experiments for decades (Baumgartner et al., 2009; Fehr & Gintis, 2007; Fehr Schmidt, 1999; Spitzer, Fischbacher, Herrnberger, Grön, & Fehr, 2007; Zelmer, 2003). A key finding is that actors' decisions are influenced by how the social dilemma is presented (Andreoni, 1995; Deutsch, 1958; Fosgaard, Hansen, & Wengström, 2014, 2015; Pruitt, 1967; Liberman, Samuels, & Ross, 2004), often referred to as *framing* (Pelphrey, Morris, & McCarthy, 2004). This violation of the so-called description invariance principle is puzzling (Camerer & Thaler, 1995), as preferences should not change relative to how the options are presented. Although it is still under debate how framing shifts decision preferences in social dilemma situations, it is possible that framing modulates neural processes associated with *mentalizing*, which is the capacity to infer the mental states of others (Dufwenberg, Gächter, & Hennig-Schmidt, 2011). Indeed, social dilemmas require actors to predict the intentions of others to deduce how they will respond to specific acts, and several behavioral studies have already suggested that mentalizing plays a crucial role in solving framed social dilemmas. For example, framing has been shown to affect how cooperative a participant expects other group members to be (Dufwenberg, Gächter, & Hennig-Schmidt, 2011) and to shape the moral assessment of free-riding behavior (Cubitt, Drouvelis, Gächter, & Kabalin, 2011). Notably, a recent report by Chang and Sanfey (2013) showed that participants' expectations about other's intentions in the ultimatum game provided a stronger explanatory power on their actual decisions compared with alternative explanations, such as inequality aversion. Still, the exact psychological mechanisms underlying these effects remain to be identified.

Mentalizing in Social Dilemmas

If mentalizing is a driving force behind framing the behavior in social dilemmas, different

measures of mentalizing should indeed reflect differences in the degree with which people are affected by framing. We conducted the present study with the aim to assess the effects of framing in social dilemmas by employing both behavioral and neurobiological measures of mentalizing. We ran two related studies using an iterated version of the prisoners' dilemma (PD) game (Axelrod & Hamilton, 1981; Gibbons, 2006) to probe whether participants engage psychological and neural processes related to mentalizing when choosing between conflicting choices in two different contextual frames (i.e., a collaboration vs. a competition frame). We first conducted a behavioral study focusing on overt measures of mentalizing, including asking the participants what they thought the other players would do. In a second experiment, we used functional MRI (fMRI) to study the neural underpinnings of the framing effect while participants played the PD game in framed contexts of collaboration and competition. We were particularly interested in identifying neural activity associated with social decisions that adhered to the social context imposed by the frame. We hypothesized that decisions that were aligned with the imposed frame (conformity), as opposed to decisions opposing the frame (nonconformity), would be associated with increased activation in the mentalizing network, specifically the superior temporal region (gyrus and sulcus), precuneus, and medial prefrontal cortex (Baumgartner, Knoch, Hotz, Eisenegger, & Fehr, 2011; Knoch et al., 2008; Mitchell, 2009; Yarkoni, Poldrack, Nichols, Van Essen, & Wager, et al., 2011). We also expected increased engagement of the hippocampal formation, as prior research has implicated this region in different kinds of framing effects (Eichenbaum, Yonelinas & Ranganath, 2007; McClure et al., 2004). Specifically, we assert that there is a fundamental difference between situations in which people are directly affected by contextual information and when they are not. Being affected by a frame is believed to be related to the involvement of a particular kind of heuristic that has a strong and direct effect on behavior. Conversely, not being affected by a frame could be the result of either the frame not triggering this heuristic, or the person being able to dispense from this response via higher-order control functions such as executive control. Together, this implies that situations in which our behav-

ior is affected by a social frame will be related to a stronger engagement of brain regions involved in social functions.

In both experiments, participants played an iterated prisoner’s dilemma game with a “stranger matching” procedure (Andreoni & Croson, 2008) where they decided whether to cooperate or not. In each trial, a grid was presented on a screen showing the financial outcomes of four combinations based on whether they chose to cooperate or defect, respectively. The grid provided information about their potential economic gains (Player A) as well as those of their interaction partner (Player B). The dominant strategy for each player is to not cooperate (Gibbons, 2006). However, the outcomes were structured such that if both players chose to cooperate, their joint outcome was maximized. Each trial was pseudorandomly framed as either a competition game or a cooperation game with the aim of swaying the participant to view the interaction with the other player as being either antagonistic or cooperative. Only the label of the game changed across frames (see Figure 1).

In the behavioral study, participants performed two tasks: in a decision phase, they

decided between Option A and B which was a choice between cooperation and defection. In a subsequent belief phase, the participants were asked to guess their opponent’s choice (indicating cooperation or defection). The participants were informed that the monetary outcomes of two randomly selected trials would be used to calculate how much they would be paid after the game. To ensure motivated efforts during the belief phase, the participants were also informed that they would receive 10 DKK (≈2 USD) for each correct belief assessment drawn from two random trials.

In the neuroimaging experiment, a separate group of participants underwent whole-brain fMRI while performing the prisoner’s dilemma game. The prisoner’s dilemma set-up was identical to the behavioral study except for two notable differences (see Figure 2). We eliminated the explicit belief phase as we were more interested to map the neural correlates of covert mentalizing when making the actual decision. We also separated the presentation of the frame information (cooperation vs. competition) from the decision phase to dissociate brain activity generally associated with the framing context from brain activity related to decision making in

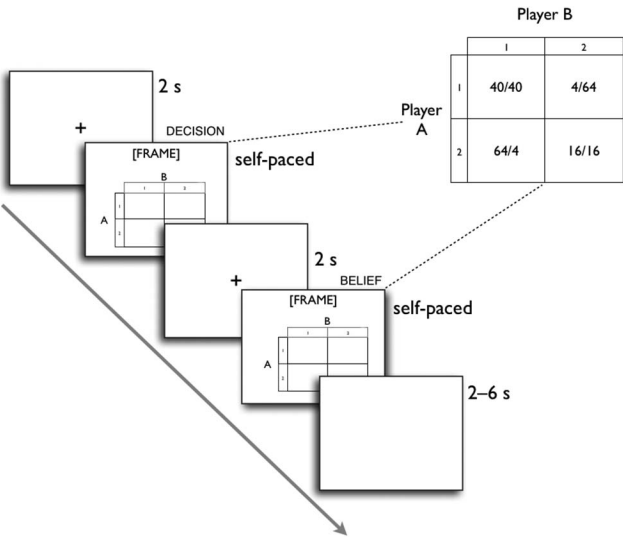


Figure 1. Experimental design of the behavioral study (A), consisting of (1) a decision phase showing the full decision matrix and (2) a belief elicitation phase. Both were organized as self-paced. The participant always acted as Player A and used the right-hand index and middle fingers to respond with Options A and B, respectively. The decision was self-paced and the decision screen disappeared after the decision was made. Our behavioral results demonstrate a clear effect of framing on cooperation and defection rates (B).

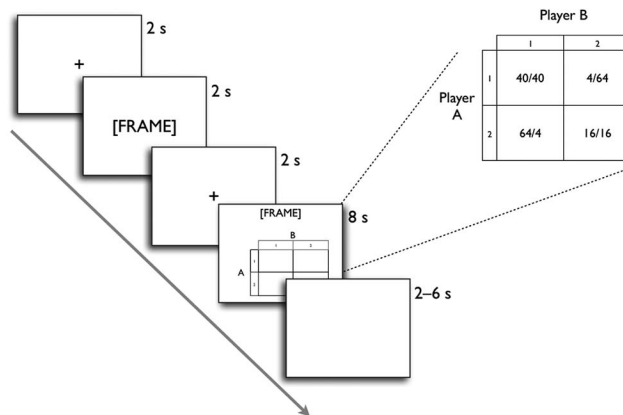


Figure 2. Experimental design of the fMRI study (A), consisting of (1) a framing phase, where participants either saw the words “cooperation” or “competition” and (2) a decision phase showing the full decision matrix wherein participants had 8 s to decide (the decision screen was present throughout the 8 s, regardless of the actual choice). Slide duration is shown in seconds.

a social dilemma. Participants were matched using a validated procedure (Baumgartner et al., 2009) and told that they had been matched with partners from the previous behavioral study, but were not provided any information about how their partners had responded. Participants participating in Study 2 were matched with some of the participants who completed Study 1. This means that the decisions of participants from Study 1 might be used twice if they are matched with test persons from Study 2. After completion of Study 1, we sought approval from participants participating to use their decisions in a subsequently experiment. The participants who agreed were also paid for the second set of decisions.

Study 1: Relationship Between Framed Decisions and Mentalizing

Method

The protocol for both studies was approved by the local ethics and adhered to the standards expressed in the Declaration of Helsinki.

Participants. Thirty participants (16 men and 14 women; age: $M = 24.7$, $SD = 9.8$) were recruited from the Copenhagen region through randomized sampling from a database of volunteers at the Department of Economics, University of Copenhagen. All participants completed the experiment in one session, which lasted

approximately 45 min. The study took place at the Laboratory for Experimental Economics, the Department of Economics, University of Copenhagen.

Experimental paradigm. Before playing the game, the participants received instruction and training for the task. Participants were told that they would be matched with a new player for each repetition of the game. Thus, participants knew that in each repetition of the game they were randomly matched with a new player. Throughout the experiment participant would not be able to see the responses of the other player. Thus, no feedback was given between the repetitions. Before the game, the participants also went through additional paper and pen tests to assess their cognitive, emotional, and interpersonal traits (see subsequent text for more details).

Participants first received standardized written instructions, which explained that they would be matched with a new person for each trial (“stranger matching”) and that they would receive a fixed payment for attending the session. Participants were also told that four randomly selected trials would be used for additional payment (see subsequent text). Each participant was positioned in front of a computer at an average viewing distance of 60 cm. Stimulus presentation and response recording (response and response time) were performed

using E-Prime 2.0 (PST Tools Inc.; see www.psnet.com) in a Windows XP environment. During the game, each trial either displayed the word “cooperation” or “competition” above the payoff matrix (see [Figure 1](#)). Participants were explicitly instructed that these words were the names of the games and that their partner received the same information. This approach followed the tradition of behavioral economics, in which participants were not instructed on any exact interpretation of the frame information, but rather provided the choice environment, and within this environment make their choice ([Chang & Sanfey, 2013](#); [Dufwenberg, Gächter, & Henning-Schmidt, 2011](#); [Liberman et al., 2004](#)). The choice of having the frame information present during the choice was also made to minimize the possibility that participants forgot the frame.

Between each trial, a fixation cross was shown for 2 s. During the decision phase, the participants responded by pressing one of two buttons to indicate their choice; in effect whether they chose to “cooperate” or “defect.” The paradigm did not put any constraints on the response times. The same buttons were used in the belief phase to indicate the anticipated choice of their opponent. Participants were informed that they would be playing against a real human being to increase the level of engagement in the game.

The experiment consisted of 56 trials, which were presented in a fixed pseudorandomized order; that is, the order of the trials was randomized during the experiment design phase but were shown in the same order to all participants. There was an equal number of cooperation and competition trials. To avoid routine behavior and increase motivation and task performance, the payoff structure was variably and pseudo-randomly scaled across trials (20%, 40%, 60%, 80%, and 100% scaling of maximum payoff). In the 100% scaling, the payoff when the opponent cooperated and the participant defected was 5 DDK (≈ 1 USD) and 80 DDK (≈ 13.5 USD), respectively; mutual cooperation earned them 50 DDK (≈ 8.5 USD) each; mutual defection earned them 20 DDK each (≈ 3.5 USD) each. Although the absolute value of the payoff varied, the relative value remained unchanged. The applied scaling was balanced across the frames and varied in a pseudorandomized manner. The screenshot presented in [Figure 1A](#) is an example of an 80% scaling. Each person’s choice option was labeled as 1 and 2, respectively, and participants made their choice by

pressing the 1 and 2 button on the PC keyboard. As a further step to ensure the participants’ full attention, the spatial order of the location of the choice options was changed in 25% of the trials. This manipulation was used to avoid automatic button pressing for any given decision. An overview of the experimental design is illustrated in [Figure 1A](#).

Behavioral data analysis. We first tested whether previously reported between-participants framing effects in social dilemmas were also present when using a within-participant experimental design. We applied Wilcoxon signed-ranks test to compare the individual degree of cooperation, the degree of beliefs regarding the interaction partner (cooperation or no cooperation), and the average response time used. This enabled us to test whether the type of frame biased the frequency distribution of participant’s decision to cooperate or not or whether the participant’s decision to cooperate or not was associated with a bias in the participant’s belief regarding the cooperation of the partner. To evaluate the importance of relations between our main variables (decision, conformity, belief, and frame) we also applied a few other tests. In particular, we used a tetrachoric correlation test, a Pearson chi-square test, and a Mann–Whitney rank sum test. The tetrachoric correlation test is designed to evaluate correlations of binary variables ([Digby, 1983](#)), whereas the Pearson chi-square test gauges the distributions of two categorical variables ([Pearson, 1900](#)), and the Mann–Whitney test is a nonparametric test which we use to compare the cooperation across frames ([Mann & Whitney, 1947](#)). The analyses were performed in the statistical software package STATA (see StataCorp LP at www.stata.com). Significance level was set at $p < .05$. Group data are reported as mean \pm one standard deviation, if not specified otherwise.

Study 2: Neural Correlates of Framed Decisions in Social Dilemmas

Method

Participants. Fourteen participants (3 male/11 women; $M \pm SD$ age = 30.5 ± 3.4) were recruited from the Copenhagen region using the same methods as in Study 1, while ensuring that enrolled participants had not participated or heard of Study 1. All participants signed an informed consent and a standardized

self-report scheme on medical history and other relevant information. Exclusion criteria included a history of or current psychiatric or neurological illness, or suspicion thereof, and factors not compatible with magnetic resonance scanning (e.g., claustrophobia, pacemaker, magnetic ligands in the body). No participants were excluded on such grounds. The fMRI study took place at the Danish Research Centre for Magnetic Resonance, Copenhagen University Hospital Hvidovre. To assess individual differences in empathic ability, participants completed an eight-item version of the empathy quotient (EQ) assessment, an assessment of empathic ability (Loewen, Lyle, & Nachshen, 2009), from which we calculated each individual's EQ score.

Experimental paradigm. The trial structure of the experimental task is illustrated in Figure 2 and differed in two aspects from the trial structure used in the behavioral experiment (Study 1). Participants had only to decide, but were not required to report their beliefs about the partner's mode of interaction. Further, the framing cue was always presented before the presentation of the grid to establish the frame (cooperation or competition) before the decision phase. As in the behavioral study, participants received instructions that these were names of the games, and that their partner received the same information, but were not instructed about the meaning of these labels. The trial structure was as follows: First a fixation cross appeared in the middle of the screen for 1 second, then participants were presented with the frame information (cooperation or competition) for 2 s. Thereafter, a fixation cross appeared in the middle of the screen for 1 s, which was followed by the grid which displayed the players' options, similar to Study 1. This grid was displayed for 8 seconds. As in Study 1, the response options were labeled 1 and 2. The participants were asked to make their choice while the grid was displayed, using their index and middle finger to press buttons on a response box to respond 1 and 2, respectively. Each trial was separated by a black screen, which was pseudo-randomly jittered for 2 to 6 s. The entire fMRI session lasted for 18 min comprising a total number of 64 trials. As in Study 1, the trials were programmed in a fixed pseudorandom order, using an event-related paradigm. All participants saw the same order of trials, with equal number of trials ($n = 32$) in each condi-

tion. As in Study 1, 25% of trials had a different variation in the choice options, allowing us to avoid habitual motor responses. This choice was made both to avoid pure automatization of choice, and to have the two studies as much aligned as possible.

With regard to the social decision, participants received the same instructions as participants who had participated in the behavioral study. However, they were not told to express their beliefs regarding the cooperation style of the interaction partner. In Study 2 we implemented a matching procedure developed by Baumgartner et al. (2009). Participants were told that they would be randomly assigned to players from a previous behavioral study (that is Study 1), but they would not be informed about how these players had actually responded. In practice we implemented this procedure by asking participants in Study 1 whether we could use their decisions from Study 1 in a later experiment and pay them again according to the outcome of their (reused) decisions and the decisions made by participants in the later study. All participants in Study 1 agreed to have their decisions reused.

Behavioral analysis. Behavioral data were analyzed and reported as described in Study 1. To further probe individual differences in behavior and brain responses, we included the EQ score as a covariate in the analysis.

Image acquisition and analysis. Participants were scanned using a Siemens Magnetom Trio 3T MR scanner with an eight-channel head coil. Consistent head placement within the scanner was ensured by orienting the head to predefined reference marks on the scanner head coil. Movement was minimized by applying cushions to fix the head in position. A scout scan was run to define the field of view (FOV) for the subsequent scans. The participants were first scanned using a structural T1-weighted MPRAGE (Magnetization Prepared Rapid Acquisition Gradient Echo) scan with a voxel dimension of $1 \times 1 \times 1 \text{ mm}^3$, FOV = 256 mm, matrix $192 \times 256 \times 256$, TR/TE/TI = 1540/3.93/800 ms, and a flip-angle of 9° . During task performance, the participants were scanned with Blood Oxygenation Level-Dependent (BOLD) fMRI using an echo planar imaging sequence (TR/TE = 2430/30 ms, 90° flip angle, 64×64 matrix, 42 slices with no interslice gap) and a voxel size of $3 \times 3 \times 3 \text{ mm}^3$. The

slices were aligned to the anterior commissure (AC) – posterior commissure (PC) line (approximately 12°).

Preprocessing and analysis of the fMRI data were performed using SPM8 (Wellcome Department of Imaging Neuroscience, London). Images were realigned without smoothing. The echo-planar image series was co-registered to each individual's AC–PC aligned structural image using mutual information, tri-linear interpolation without warping, and was subsequently checked manually. Images were normalized to the Montreal Neurological Institute (MNI) template and smoothed using a Gaussian kernel with a full-width at half-maximum of 8 mm. The first two volumes of each session were discarded to allow for T1 equilibration.

The individual fMRI time series were analyzed using multiple regression analysis (general linear model) with separate event regressors for the frame information phase, the decision-making phase (when participants were presented with the response options), and motor responses (modeled at the time of the button press; duration = 0). Rest was not modeled independently. The regressors were convolved with a canonical hemodynamic response function. We also accounted for artifacts caused by head movement, pulse and respiration by including an additional 24 nuisance regressors in the first-level analyses.

For the decision-making phase, we modeled the combinations of a 2 (framing: cooperation, competition) \times 2 (behavior: defect, cooperate) factorial design. For the construction of regressors of interest, we let α be the cooperation frame, β be the competition frame, and x and y as cooperate and defect behaviors, respectively. Thus, we constructed four regressors of interest at the first-level analysis: α_y , α_x , β_x and β_y . To study the general relationship between frame conformity and brain activation, we analyzed the instances in which participants aligned their choice to the frame, using the following model:

$$[(\alpha_x - \alpha_y) + (\beta_y - \beta_x)]$$

In addition, our study design allowed us to explore the neural correlates of frame nonconformity, that is, when the participant's decision violated the mode of social interaction as imposed by the frame. To study the neural engagement during nonconform choices we analyzed

both instances of nonconform behaviors, that is, $[(\alpha_y - \alpha_x) + (\beta_x - \beta_y)]$.

After testing our a priori hypotheses, a post hoc analysis was run to test for an additional modulatory role of individual empathy scores according to the EQ questionnaire (Loewen et al., 2009). We tested the univariate regression of empathy scores on neural engagement for the conformity > nonconformity contrast and then on the nonconformity > conformity contrast.

Finally, we studied the effects of framing on neural activation by analyzing only the framing phase. Here, we modeled the cooperation frame and competition frame as independent regressors. Paired t tests were run for competition > cooperation and cooperation > competition.

Regarding frame conformity, our primary neuroanatomical hypothesis concerned whether or not framing would engage brain regions critical for either *mnemonic* processing, that is, structures in the hippocampal region (De Martino, Kumaran, Seymour, & Dolan, 2006; Eichenbaum, Yonelinas, & Ranganath, 2007; McClure et al., 2004), or *mentalizing* processes, that is to say structures such as, for example, precuneus, the temporo-parietal junction, superior temporal regions, and ventromedial and dorsomedial prefrontal cortex (PFC; Baumgartner et al., 2011; Iacoboni et al., 2004; Mitchell, 2009; Yarkoni et al., 2011). We therefore defined regions of interest (ROI) using a 10 mm radius centered in peak voxel coordinates reported by previous studies. The hippocampus ROI was defined using the coordinates from McClure et al. (2004): (left hippocampus $x, y, z = -24, -24, -20$ and right $x, y, z = 20, -20, -16$). The definition of mentalizing ROIs was guided by a review of the neural bases of mentalizing (Mitchell, 2009) and we used reported peak coordinates from a Neurosynth meta-review based on 33 neuroimaging studies categorized by the term *mentalizing* (see <http://neurosynth.org/analyses/terms/mentalizing/>). The mentalizing ROIs were defined as 10 mm radius spheres with a center in the following xyz-coordinates: precuneus (0, -52, 36), ventromedial PFC (0, 48, -16), dorsomedial PFC (0, 32, 52), the left and right temporo-parietal junction (-52, -56, 20 and 52, -56, 20), and superior temporal region (-56, -4, -20 and 56, 2, -20).

Clusters from frame conformity and linear regression analysis were considered significant

at $p < .05$ after correction for multiple comparisons using familywise error correction (FWE) within the predefined ROIs (the voxel extent threshold prior to small volume correction was set at $p < .001$ uncorrected). Activated regions outside the predefined ROIs were considered significant at the cluster level applying a significance criterion of $p < .05$ after FWE correction across the whole brain. We also considered as trend activations clusters with a $p < .05$ uncorrected for multiple comparisons.

Results

Study 1: Relationship Between Framed Decisions and Mentalizing

Participants earned 139 DKK (≈ 26 USD) on average, including an attendance fee of 50 DKK. In the decision phase, participants took an average of 9.94 (0.41) seconds to decide. Conformity ($\alpha_x + \beta_y$) did not differ in response times compared to nonconformity ($\alpha_y + \beta_x$; Wilcoxon's signed-rank $z = -1.64$, $p = .101$). Similarly, in the second phase—the belief phase—the average response time was 2.78 (0.12) seconds, and the frame manipulation did not significantly affect response time (Wilcoxon's signed-rank $z = -0.46$, $p = .649$).

Table 1 provides an overview of the choices and expected choices (belief) of others, and Figure 3 illustrates the individual conformity rates across the frames. Overall the cooperation rate was 29% in the competition frame, compared to 61% in the cooperation frame. A Wilcoxon signed-ranks test ($z = 4.07$, $p < .001$) reveals that the individual cooperation rates were significantly different across frames. The

cooperation rates correspond to an overall conformity rate of 61% in the cooperation rate but 71% in the competition frame. The individual conformity rates are illustrated in Figure 3 and it is evident that there exists a large variation as to how the frame information influenced participants' choices. Some participants always conform to the frame, whereas other never do. Framing also significantly affected participants' belief regarding the behavior of the interaction partner (Player B): On average, the expectation that Player B's decisions would be cooperative was 50% in the competition frame, but was 65% in the cooperation frame (Wilcoxon signed-ranks test: $z = 3.43$, $p = .001$). There was a significant relationship between this belief and the participant's own choices, as illustrated in Table 1 (tetrachoric $\rho = 0.43$, $p < .001$, $\chi^2(1) = 127.691$, $p < .001$). Independently of the frame, 55% of defection choices were accompanied by the belief that Player B would also defect. Conversely, only 28% of cooperation choices were accompanied by a belief that Player B would defect. In other words, participants' actions were significantly affected by their assumptions about the other player's frame of mind, and this assumption, in turn, were significantly modulated by the frame information. When choosing to defect, participants reported a significantly higher belief that Player B would defect during the competition frame (59%) than during the cooperation frame (48%; tetrachoric $\rho = 0.18$, $p = .001$). No such relation was found for cooperative choices: The expected degree of cooperation was 71% in the competition frame and 73% in the cooperation frame (tetrachoric $\rho = 0.02$, $p = .795$).

Table 1
Overview of Behavioral Results in Study 1

	Both frames	Competition frame	Cooperation frame
Cooperation rate and belief about cooperation across frames			
Cooperation rate ^a	44.9% (.49)	29.2% (.45)	60.6% (.49)
Conformity rate ^b		70.8% (.45)	60.6% (.49)
Belief of cooperation	57.0% (.50)	49.5% (.50)	64.5% (.48)
Average belief of defection			
When defecting	55.3% (.49)	59.5% (.49)	47.7% (.50)
When cooperating	27.9% (.45)	28.6% (.45)	27.5% (.45)

Note. Numbers in parentheses are standard deviations.

^a Cooperation rate is the relative occurrence of cooperation choices. ^b Conformity rate is the relative occurrence of conforming choices (aligning choice and frame).

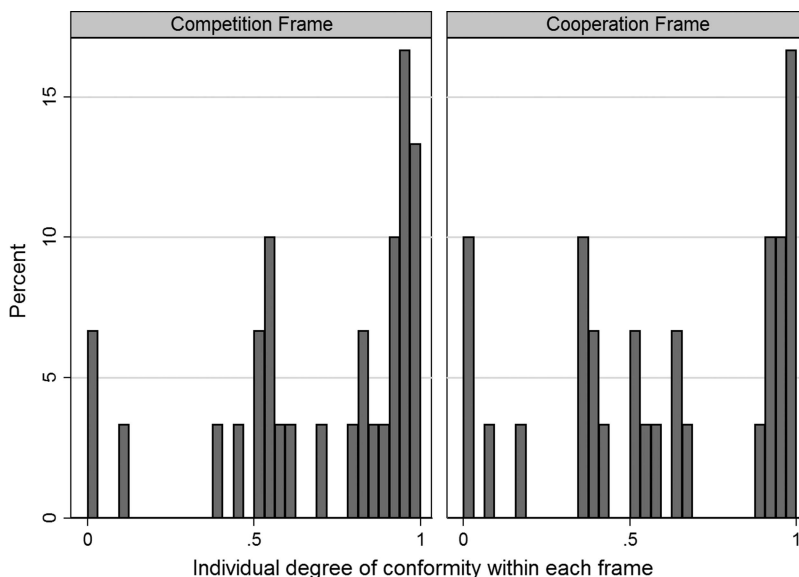


Figure 3. The degree of conformity at the individual level in Study 1, across the frames, ranging from no conformity (0.0) to full conformity (1.0). A decision is considered to conform if the cooperative choices are taken in the cooperation frame and the defection choices are taken in the competition frame. The individual measure is the degree to which the participant takes conform choices.

Study 2: Neural Correlates of Framed Decisions in Social Dilemmas

Analysis of the behavioral data obtained during fMRI yielded a significant within-participant framing effect (Mann–Whitney test $z = -6.82$, $p = .000$) replicating the result that had been obtained in the behavioral experiment (Study 1).¹ In the competition frame, 31% of the decisions were cooperative, while 54% of the decisions were cooperative in the cooperation frame. We found that there was a significant relation between conformity of the choices and the frames (tetrachoric $\rho = -0.228$, $p < .001$). Overall, conformity rate was 68% in the competition frame as opposed to 54% in the cooperation frame. Individual conformity rates across the frames are illustrated in Figure 4; in parallel with Study 1 large variation is observed. The degree of conformity with the frame was found to vary substantially across participants, ranging from 6.25% to 100%, where a score of 100% means that the participant always behaves according to the frame. The average response time of decisions was 3.4 ± 0.05 seconds, and did not differ be-

tween frames (Wilcoxon signed-ranks test: $p = .581$) or decision types (Wilcoxon signed-ranks test: $p = .424$).² Notably, the average response time in Study 2, where participants had to respond within 8 seconds, was shorter than in Study 1 (9.94 ± 0.04 s), where responses were self-paced.

Confirming our main neurobiological hypothesis, frame conformity was associated with a significantly stronger bilateral activation of the hippocampal formation and parts of the mentalizing network, including the lateral temporal cortex, precuneus, and the dorsomedial PFC (see Table 2). Notably, this activation pattern was present for both the competition frame

¹ Comparing the individual levels of cooperation across frames a Mann–Whitney test also finds a significant difference ($z = 1.931$, $p = .054$), and similarly a Wilcoxon signed-ranks test also find a significant difference ($z = 1.759$, $p = .079$).

² The reaction time (RT) was 3.45 s (1.71) in the competition frame, and 3.39 s (1.50) in the cooperation frame. Across the decision types, the RT was 3.46 s (1.50) for defection choices and 3.54 s (1.60) for cooperative decisions. The numbers in the parentheses are the standard deviation.

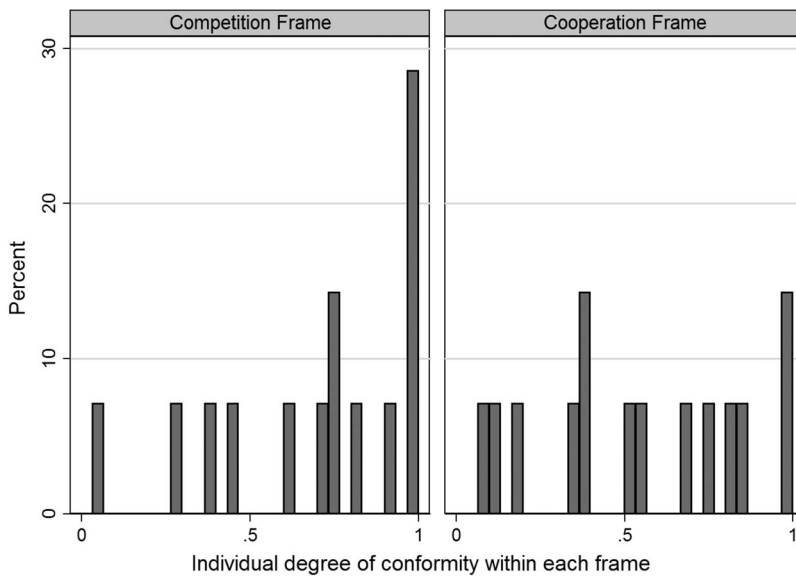


Figure 4. The degree of conformity at the individual level in Study 2, across the frames, ranging from no conformity (0.0) to full conformity (1.0). A decision is considered conform if the cooperative choices are taken in the cooperation frame and the defection choices are taken in the competition frame. The individual measure is the degree to which the participant takes conform choices.

and the cooperation frame, demonstrating that the engagement of these regions was associated with increased likelihood of conformity with the frame (see Figure 5). Other regions of the mentalizing network, such as the temporo-parietal junction and the ventromedial PFC, did not show a relationship with conformity.

To test for additional modulation of individual differences in mentalizing, we ran a post hoc analysis in which each participant's score on a self-report empathy questionnaire was included as a covariate, first for the conform–nonconform contrast and the subsequently for the converse contrast (nonconform > conform). We tested whether individual differences in empathy score predicted decision-related neural activation. Within the predefined ROIs, only one region showed a significant effect between empathy and neural activation. The decision-related activation of left hippocampus showed a positive linear relationship with the individual level of empathy and for conforming as opposed to nonconforming decisions ($x, y, z = -34, -30, -16, z = 3.63, p < .05$ FWE).

The whole brain exploratory analysis testing neural engagement during frame conformity re-

vealed a widespread network of regions involved in decisions to conform versus to not conform to the frame (see Table 3). We further ran a post hoc whole brain analysis to test for differences between the two kinds of frame congruency (congruency–cooperation vs. congruency–competition). Here, we found no significant differences, even at a liberal threshold ($p < .01$, uncorrected).

While framing facilitated frame conformity, participants sometimes made decisions that violated the frame. This enabled us to test for brain regions showing increased neural activity associated with nonconforming decisions that would violate the expectation of how the other player would respond. This exploratory analysis yielded a significant engagement of the left angular gyrus for frame nonconformity as opposed to frame conforming decisions. Clusters in the inferior frontal cortex, superior parietal cortex, and temporo-parietal cortex displayed a similar trend toward stronger activation for nonconformity decisions ($p < .001$, uncorrected; see Table 3).

Because participants in both Studies 1 and 2 showed a relatively stronger susceptibility to the framing effect in the competition frame than

Table 2
Results of the Regions of Interest (ROI) Analysis During Choice Conforming to the Frame (Contrast: Conformity > Nonconformity)

Region and hemisphere	Coordinate	<i>z</i>	Cluster <i>p</i> _{FWE}
Lateral temporal cortex			
Right	56, 2, -20	4.81	.002
Precuneus			
Medial	0, -52, 360, -56, 42	4.31	.001
Dorsomedial prefrontal cortex			
Medial	0, 32, 52	3.25	.022
Hippocampus			
Right	20, -20, -16	4.28	.001
Left	-24, -24, -20	3.68	.014

Note. The defined 10-mm radius regions of interest used for small volume corrections are presented with the center coordinate and family-wise error-corrected cluster *p* values and *z* statistics of the peak voxel within.

the cooperation frame, one possibility would be that mentalizing activation would be more prominent during the competition than the co-operation phase. To address this, we ran an exploratory analysis of the competition > co-

operation conditions during choice events. Here, we find that only the right supramarginal gyrus showed a significant difference (26, -30, 32, *z* = 3.47, *p* < .001 uncorrected, 19 voxels). For the converse contrast (cooperation > com-

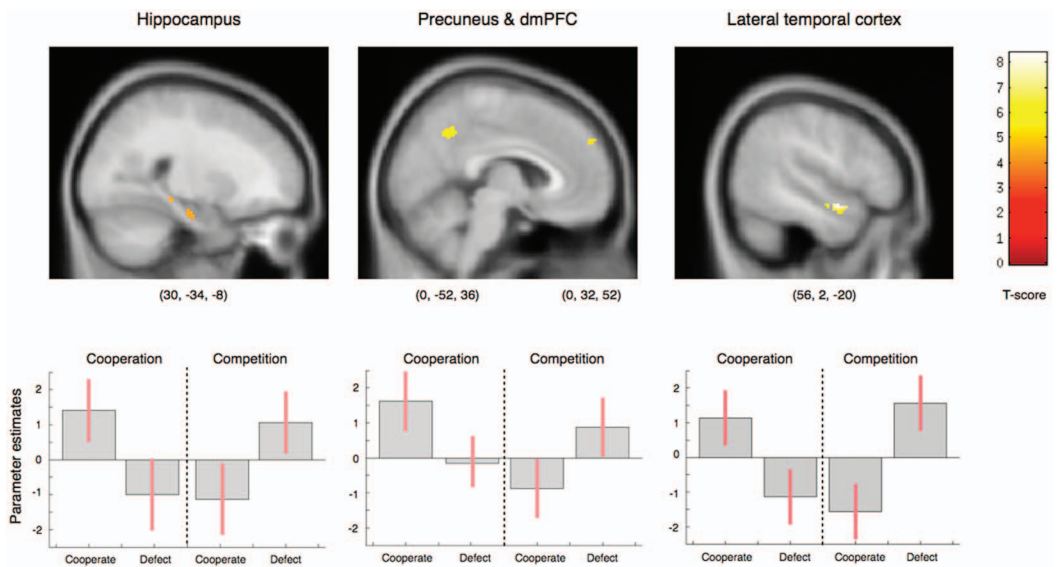


Figure 5. Brain activity related to frame conformity in the prisoner's dilemma game. Upper panel: Statistical parametric map of brain regions showing increased regional activation during frame conformity as opposed to frame-nonconformity. For display purposes, the maps are thresholded at *p* < .001 uncorrected. Decisions conforming to the social frame caused stronger engagement of the hippocampal formation, precuneus, lateral temporal gyrus, and the dorsomedial PFC. Lower panel: Parameter estimates of the effect size for each decision condition are plotted for the voxel displaying regional peak activation for frame conformity decisions. Numbers on top indicates selected regions of interest center voxel. Bars correspond to the mean value and error bars indicate the 90% confidence interval of the mean. See online article for color version of this figure.

Table 3
Results From Whole-Brain Analysis That Contrasted Conformity or Nonconformity to the Frame

Region and hemisphere	Coordinate	Voxels	<i>z</i>	Cluster <i>p</i> _{FWE}
Conformity (conform > nonconform)				
Caudate nucleus				
Left	−10, 17, 11	2142	6.38	.001
Posterior insula				
Right	42, −14, 18	553	5.89	.001
Left	−40, −28, 26	1258	5.79	.001
Inferior frontal gyrus				
Right	32, 30, 16	1455	5.59	.001
Occipital cortex				
Left	−20, −74, 12	565	5.53	.001
Superior temporal cortex				
Right	50, 8, −4	1218	5.30	.004
Nonconformity (nonconform > conform)				
Angular gyrus				
Left	−52, −74, 18	82	4.86	.05

Note. The coordinates represent the peak voxel within respective activated clusters with *z* statistics, number of voxels in the cluster, and family-wise cluster *p* values.

petition during the choice phase) no brain region were significantly more engaged, even at a liberal threshold (*p* = .05).

We also explored the impact of the framing cue on the neural activity elicited at the time that the cue was presented. Relative to the cooperation cue, the competition cue elicited a trend activation (whole-brain *p* < .001, uncorrected, extent threshold = 5 voxels) in a number of brain regions, including the precuneus, caudate nucleus, anterior cingulate cortex and dorsolateral prefrontal cortex (see Figure S1 in online supplemental materials and Table 4). In contrast, no voxel in the brain showed stronger neural activation in response to the cooperation cue as opposed to the competition cue.

Discussion

This study provides the first combined behavioral and neurobiological account of the effects

of framing in social dilemmas. Besides confirming the effect of framing on PD behavior (Andreoni, 1995; Cubitt et al., 2011; Deutsch, 1958; Park, 2000; Pruitt, 1967; Liberman et al., 2004) our behavioral data also imply that participants based their decisions, at least in part, on how they assumed the other actor would act. This finding supports the notion that mentalizing is an important psychological process during decision making in social dilemmas (Frith & Singer, 2008). It is important to note that this effect appeared to lead to different behavioral strategies in the two frame conditions: If the actor (Player A) believes that the opposing person (Player B) will defect, Player A will feel compelled to defect, too. In the cooperation frame, the increased belief that the other player will collaborate prompts two types of responses. Most actors take the frame-congruent choice and follow the generally expected behavior and choose to cooperate. However, some also

Table 4
Cooperation Rate and Conformity Rate Across in Study 2

	Both frames	Competition frame	Cooperation frame
Cooperation rate ^a	43.1% (.50)	31.6% (.47)	54.4% (.50)
Conformity rate ^b		68.4% (.47)	54.4% (.50)

Note. Numbers in parentheses are standard deviations.
^a Cooperation rate is the relative occurrence of cooperation choices. ^b Conformity rate is the relative occurrence of conforming choices (aligning choice and frame).

choose to “free-ride” on the expected cooperative choices made by the other player, and thus, to violate the implicit social expectancy of collaboration.

In agreement with the behavioral data, fMRI revealed a consistent activation of the hippocampal formation and regions known to be in mentalizing when participants made decisions that conformed to the imposed frame. Besides confirming the significant effect that framing had on cooperation levels during game play, the fMRI results yielded increased activation of the bilateral hippocampal formation and the brain’s mentalizing network for frame conforming relative to nonconforming decisions. In addition, the individual level of empathy was associated with increased activation in the left hippocampal formation during frame-coherent decisions, adding further support to the notion that this structure is significantly related to the effects of framing in social dilemmas. The hippocampal formation is known to play a key role in memory and associative functions (McClure et al., 2004), which suggests that framing effects are related to a stronger engagement of this mnemonic system. Accordingly, neuroimaging studies of decision-making and the influence of contextual information have implicated the hippocampus and surrounding regions (De Martino et al., 2006; Frith & Frith, 2006).

In addition to the hippocampus, brain regions known to be involved in mentalizing, such as the lateral temporal gyrus, precuneus, and the dorsomedial prefrontal cortex showed stronger activation for frame conformity as opposed to nonconformity. The lateral temporal cortex and precuneus are thought to be particularly important to processing social information and has been linked to mentalizing and social cognition in many imaging studies (Baumgartner et al., 2011; Mitchell, 2009; Yarkoni et al., 2011). Furthermore, the medial PFC has been implicated in social choice such as altruism, norm compliance and responses to undesirable social actions (Knoch et al., 2008; Knoch, Pascual-Leone, Meyer, Treyer, & Fehr, 2006; Knoch, Schneider, Schunk, Hohmann, & Fehr, 2009). Our data extend the role of these structures to include the processing of contextual information and its influence on behavior in social dilemmas, yet further research is needed to disentangle the precise functional roles that these regions may have in this process.

When participants acted in opposition to the frame, there was enhanced engagement of left angular gyrus. Similar trends toward increased activity for frame-nonconforming decisions were found in the inferior frontal cortex, superior parietal cortex, and temporopolar cortex. Prior studies have demonstrated a role for the inferior parietal cortex and inferior frontal cortex in social decision making, including social reasoning (Baumgartner et al., 2011), norm violation (Mitchell, 2009) and reward expectation (Baumgartner et al., 2009), and recent studies have implicated the angular gyrus in social reasoning and moral behavior (Yarkoni et al., 2011). Our study adds to this knowledge by including behavior in which an agent acts in opposition to contextual instructions and, in particular, behavior elicited by situations in which the agent stands to benefit by violating expectations in social dilemmas.

Finally, exploratory analyses revealed that the frame cue elicited stronger activation of the precuneus, caudate nucleus, anterior cingulate cortex, and dorsolateral prefrontal cortex for competition cues as opposed to cooperation cues. Notably, because our interstimulus interval was 1 s and nonjittered, this exploratory analysis cannot reliably distinguish between the framing and decision phase, and the results can only be seen as tentative trends. Nevertheless, when making the same comparisons during the decision phase, only the right supramarginal gyrus showed a stronger engagement during competition relative to cooperation framing. These observed trends may suggest that the regions already implicated in framing effects (Deppe et al., 2007; McClure et al., 2004) may be engaged already at the time of framing and before decision options have been presented. Furthermore, these data support previous reports of a role for the right PFC in social decision making (Knoch et al., 2006) as well as the engagement of anterior cingulate cortex in frame susceptibility (Deppe et al., 2007). The present results expand this knowledge showing that a contextual frame can be established instantly and independent of a presented response option and the type of decision made (i.e., cooperative or deceptive decisions). In contrast, the cooperation instruction was not associated with a specific neural response pattern compared with the competition frame. This suggests that framing a social dilemma as a competition

will more strongly activate neural structures that are related to the context dependency of social decisions compared with cooperative framing. One might speculate that this is caused by the competitive frame being considered as being more important or challenging than the cooperation frame. Indeed, recent studies have demonstrated that cooperative behaviors may represent a social “default mode” of decision making in similar conditions (Loewen et al., 2009; Rand, Greene, & Nowak, 2012; Rand, Newman, & Wurzbacher, 2015; but see also Rubinstein, 2007, for contradictory findings). By the same token, when expecting competition, participants deviate from this social default and more strongly engage in expectation and mental calculation and mentalizing.

Taken together, our combined behavioral and neuroimaging data suggest that framing in social dilemmas work by invoking a social mnemonic heuristic where participants choose their behavioral responses based on how they think their opponents will act. Our exploratory analysis of the framing stage hints at the possibility that such framing effects may occur even before decision options are perceived, although more studies are needed to confirm this assertion. As such, the study illustrates the complexity of decision making in social dilemmas, in which humans either adhere to contextual cues, or choose to violate the tentative instruction embedded within those cues.

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