



You cannot gamble on others: Dissociable systems for strategic uncertainty and risk in the brain

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ABSTRACT

This paper tests whether strategic uncertainty employs circuits in the brain that encode risk and utility, or circuits that are involved in Theory of Mind (ToM). We compare participants' decisions in a stag-hunt game with an equivalent choice between Bernoulli lotteries where the probabilities are equal to the mixed Nash equilibrium of the stag hunt game. Behavioral data suggests that most participants are more willing to choose the payoff-dominant option in a stag-hunt game than the equivalent lottery. Neuroimaging shows that activations in the regions of the brain commonly associated with ToM are correlated with a participant's propensity to choose payoff dominant. This suggests that individuals who mentalize the other person are more likely to be cooperative than those who do not.

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1. Introduction

The gains from cooperation can be immense. When individuals are uncertain of others' commitment to a task, cooperation often fails. This uncertainty of another person's actions is referred to as strategic uncertainty. Economists have debated whether strategic uncertainty is a function of converting the other players' payoffs into probabilities of their actions and making an assessment of the risk. Game theorists and economists have argued that individuals are unlikely to randomize and equally unlikely to believe that others randomize (Radner and Rosenthal, 1982; Aumann, 1987; Huyck et al., 1990; Rubinstein, 1991). The extent to which strategic uncertainty differs from risk in the brain has not been studied. This paper seeks to find neural substrates that are unique to strategic uncertainty by contrasting it with tasks involving only risk.

Rousseau's stag hunt story encapsulates the incentives of strategic uncertainty. In his story, two hunters set out to hunt a deer. Each man must keep a post in order to capture a deer. While one hunter is manning his post, a hare passes in front of him. At this point the hunter is faced with a decision: continue to man his post or attempt to chase the hare. Both hunters would rather have the deer than the hare; the deer provides the greatest amount of food for both hunters. The only reason for the hunter to chase the hare is if he believes the other has abandoned his post in an attempt to capture smaller game. In other words, if one hunter fears the other hunter will abandon his post, then his best response is to chase the hare (Skyrms, 2001).

What is puzzling in Rousseau's story, which is the inspiration behind the stag-hunt game, is that it lacks a direct incentive to be uncooperative. Unlike the prisoner's dilemma game, in which it is profitable to be uncooperative; uncooperative behavior in the stag hunt game is a consequence of mistrusting the other player's motivations. Cooperation has the greatest payoff, both socially and individually; but the mistrust of each other's motives leads the players to forgo the optimal outcome

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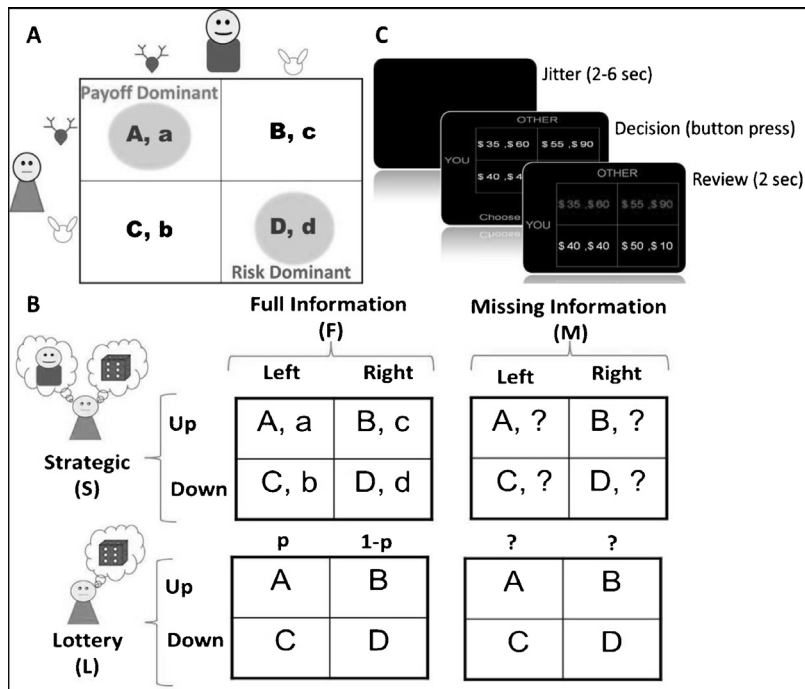


Fig. 1. (A) Standard normal-form stag-hunt game where $A > C \geq D > B$ and $a > c \geq d > b$. Shaded circles around payoffs indicate the Nash equilibria. (B) Game matrices presented in each treatment. The probabilities (p) in lottery treatment are the mixed Nash equilibrium probabilities from the equivalent person treatment. Note that the person treatment can invoke ToM networks, risk and utility circuits, or both; while the lottery only invokes the risk and utility circuits. (C) Screen shots of game played in scanner. Jitter was a blank screen present for 2–6 s uniformly distributed. Decision screen lasted until the subject responded. The review screen, which highlights the decision, was displayed for 2 s.

in return for something sure. The uncertainty present in this game is considered strategic uncertainty, and has been a topic of interest to theorists and experimentalists alike (Harsanyi and Selten, 1988; Huyck et al., 1990).

In game theory, the stag hunt game is a simultaneous game with complete information that can be expressed in matrix form (Fig. 1A), where (stag, stag) and (hare, hare) are both Nash equilibria in pure strategies. One of these equilibria (stag, stag) is referred to as the payoff dominant, because it offers the greatest reward to both players. But the payoff structure of the game does not provide a clear prediction of other players' behavior. With respect to the pure strategy equilibria, one would expect rational players to choose the payoff dominant equilibrium (stag, stag), yet this choice is risky. Indeed, Harsanyi and Selten (1988) introduced an alternative criterion, the risk dominant, to account for the risk of disequilibrium.

The payoff dominant equilibrium expresses a player's desire to maximize his payoffs, which is also Pareto optimal. Since (stag, stag) has the greatest payoff, players who seek to maximize their payoffs attempt to coordinate on the (stag, stag) Nash equilibrium. The risk dominant equilibrium expresses a player's desire to "play it safe" or minimize the cost of failing to coordinate on one of the two Nash equilibria. Consider the game in Fig. 1A. The payoffs are such that $A > C \geq D > B$ and $a > c \geq d > b$. If the column player unilaterally chose to move from (stag, stag), the row player would pay a greater opportunity cost than if he were to unilaterally move from (hare, hare). As such, the cost of failing to coordinate on (stag, stag) is greater than the cost for failure to coordinate on (hare, hare). If a player is unsure of the other player's motives, he risks less by choosing hare than by choosing stag. Therefore, the hare option is the risk dominant equilibrium.

The choice of risk dominance over payoff dominance is attributed to strategic uncertainty, but it is unclear if strategic uncertainty is a matter of risk preferences or strategic mistrust of the other player's actions. Straub (1995) argued that the strategic uncertainty is strictly different from risk preferences, but it is possible that players convert the uncertainty of the other player's decision into a game against nature or a lottery. If this is the case, the mechanisms used by individuals to evaluate random events can be applied to games with strategic uncertainty.

There are many experimental studies with the stag hunt game (Huyck et al., 1990; Straub, 1995; Rankin et al., 2000; Battalio et al., 2001), but to study the neural substrates unique to strategic uncertainty we must resort to techniques in neuroscience. Using functional magnetic resonance imaging (fMRI), we are able to observe which regions of the brain are active during strategically uncertain decisions. Although fMRI data does not prove a specific region causes a particular behavior, correlating strategically uncertain decisions with brain activity can expose latent neural circuits actively involved in the task.

Studies have shown that the encoding of risk and utility is fairly localized to specific brain regions. The ventral striatum has been shown to encode the magnitude of a monetary reward in both random and non-random outcome experiments (Breiter et al., 2001; Knutson et al., 2001; O'Doherty et al., 2004; Abler et al., 2006). When varying the probability of an

outcome, the ventral striatum also encodes the likelihood of a particular outcome occurring (Kuhnen and Knutson, 2005; Dreher et al., 2006; Abler et al., 2006). These results are generalizable to primary rewards, such as food (Pagnoni et al., 2002; McClure et al., 2003). Similarly, the vmPFC has been implicated in encoding the magnitude of random events when a reward was given, but was unexpected (Knutson et al., 2001; Ramnani and Owen, 2004). Other studies have shown the vmPFC engaged in goal-directed decisions, intertemporal choice, and choice consistency (Fellows and Farah, 2007; Kable and Glimcher, 2007; Hare et al., 2009). Since both strategic uncertainty and risk require the evaluation of uncertain outcomes, these regions should be active in a strategically uncertain game, such as the stag hunt.

Neuroscientists have argued that there are innate cognitive circuits that facilitate interactions with others (Baron-Cohen, 1989; Corcoran et al., 1995). Commonly known as the Theory of Mind (ToM) networks, these circuits help individuals generate predictions of others' actions. ToM tasks, such as the false belief task and prisoners dilemma games, have shown that several regions of the brain are commonly involved¹ in mentalizing another person. These areas include the medial prefrontal cortex (mPFC), lateral prefrontal cortex (LPFC), superior temporal sulcus (STS), temporal parietal junction (TPJ), temporal poles, fusiform gyrus, and both the anterior cingulate cortex (ACC) and the posterior cingulate cortex (PCC) (Carrington and Bailey, 2009). Strategic uncertainty fundamentally differs from risk by the presence of another player. As such, regions common to ToM should be present in strategic uncertainty decisions.

We seek to understand the differences between strategic uncertainty and risk. We designed an experiment which compares a strategically uncertain game with an economically equivalent choice between lotteries. We use the frequency that payoff dominant was chosen in each task to measure the extent to which an individual differentiates between strategic uncertainty and risk. Moreover, we use fMRI data to map the neural circuits that are present in strategic uncertainty, but not in risk. Even with a considerably literature on ToM, there continues to be a debate over which of the ToM regions are necessary to mentalize another person rather than evaluating a complex decision. The study of strategic uncertainty and how it differs from risk contributes to this debate. Removing processes found in risk evaluation from those involved in strategic uncertainty controls for the circuits which evaluates risk and ambiguity. But to understand the neural structures associated with strategic uncertainty, we must also control for the inherent evaluation of risk and uncertainty not due to the other player.

2. Methods

2.1. Treatments

We used a 2×2 factorial, within-subject design. In the first factor, the participant either played a Stag Hunt game with another person (P) or chose between two lotteries (L). In both cases, the possible payoffs for each outcome were the same. In the Person treatments, the participants were shown a standard normal-form game matrix (Fig. 1B). In the matrix, the participant's payoffs were the values to the left of the comma within each cell (A), while the other player's value was to the right of the comma (a). The participant was always player 1 and had the choice of Up or Down. The player 2's decisions were registered by another participant before the experiment began.

In the stag-hunt game, players are faced with a payoff dominant choice and risk dominant choice. In the payoff dominant choice, the player can maximize his earnings if their partner coordinates with them, but they receive the lowest payoff otherwise. In the risk dominant choice, the player receives less than the maximum of the payoff dominant choice, but receives more than the worst outcome regardless of their partner's decision. If the player trusts their partner to coordinate with them, then their best option is to choose the payoff dominant option. If they are unsure of the partner, then their best option is to choose the risk dominant option. Unlike the prisoner's dilemma game, there is no direct incentive to choose the non-cooperative option. Thus, the choice of risk dominant relates to a player's uncertainty of the other player's choice.

In the Lottery treatments, participants chose between two lotteries. The lotteries were displayed as a matrix with an up or down decision (Fig. 1B). The Up decision was a lottery with outcomes A or B and the Down decision was a lottery with outcomes C or D. The probability of each outcome was displayed at the top of the columns. These probabilities were based on the mixed Nash equilibrium probabilities from the equivalent strategic game matrix. The outcome of the chosen lottery was determined by dice at the end of the experiment.

We used the standard method for calculating the mixed Nash equilibrium probabilities. That is, we set the probabilities such that a risk-neutral participant would be indifferent between the choosing Up and Down. In this case, we set the probability of the other player choosing right as p and the probability of choosing left as $1 - p$. We calculated the probabilities by setting the expected value of choosing Up equal to the expected value of choosing Down and solving for p . If the Up decision has a possibility of A and B and the Down decision has a possibility of C and D (see Fig. 1A), when we set the two choices equal to each other, we find (1). By solving for p , we find (2).

$$Ap + B(1 - p) = Cp + B(1 - p) \quad (1)$$

¹ We define commonly involved as more than $\frac{1}{4}$ of the ToM experiments found activations in the region (Carrington and Bailey, 2009).

$$p = \frac{D - B}{A - C + D - B} \quad (2)$$

Similar to the stag-hunt game, the choice between lotteries has a payoff dominant and risk dominant decisions. Since both lotteries have the same expected value, the difference between the lotteries is the variance. The payoff dominant lottery has a higher possible payoff, but the variance is larger. The risk dominant lottery has a lower possible payoff, but the variance is smaller. As such, risk preferring participants should prefer the payoff dominant choice while risk adverse participants should prefer the risk dominant choice.

The second factor was whether the participant was provided with all the information regarding the other player's payoffs. When there was full information (F), participants were given the payoffs of the other player in the person treatment and the probabilities of each outcome in the lottery treatment (Fig. 1B). When there was missing information (M), a "?" was substituted for the payoffs of the other player in each cell during the Person treatments or the probabilities at the top of the column in the Lottery treatments.

In total there were 4 treatments: person with full information (PxF), person with missing information (PxM), lottery with full information (LxF), and lottery with missing information (LxM). Each treatment contained the same 56 payoff matrices with a variety of payoff incentives. That is, we make the payoff-dominant and risk-dominant more attractive in some trials and less attractive in others. Thus, if there was a stag hunt game with possible payoffs \$50 or \$0 for the payoff dominant choice and \$20 or \$30 for the risk dominant choice, then there was a choice between a lottery with possible outcomes \$50 or \$0 and another lottery with outcomes \$20 or \$30. In addition, we included both symmetric and asymmetric payoffs, and varied the matrices with respect to the mixed Nash equilibrium probabilities. We varied the matrices rewards and probabilities within treatment to ensure the robustness of our findings (see Appendix).

2.2. Procedures

We recruited 30 healthy participants from Emory University (M: 12, F: 18, age: 18–40). Participants provided written consent and were given written instructions with a verbal overview. Participants were told that they were playing a game with another person when they were presented with a matrix of payoffs separated by commas in each cell (see Appendix: Instructions) and that they were choosing between lotteries when a matrix of payoffs with the probabilities of the outcomes in the column headings was presented. Participants were not given information concerning who the other players were or any demographic information about the other player.

Participants had an opportunity to practice the task with the input device² while in the scanner. Following the practice, participants completed 4 runs, each consisting of 56 trials. In each run, there were 8 blocks of 7 trials. All trials within a block had the same treatment. Each block of a particular treatment was repeated twice per run and each treatment block was separated with a block of another treatment. This ensured that the observations were balanced in each run. Each game matrix was repeated in each of the treatments, but each matrix was only displayed once per run. The time of each trial varied based on the response of the participant.

In each trial, there were three phases. The first phase displayed the game matrix to the participant (Fig. 1C). The participant was then given the option to choose Up or Down. Payoff dominant and risk dominant choices rotated such that the Up choice was not always payoff dominant and the Down choice was not always risk dominant. Participants moved to the second phase once they completed their decision in the first phase. In the second phase, the participant's choice was highlighted for 2 s (Fig. 1C). In the third phase, a blank screen was shown for 2–6 s randomly chosen from a uniform distribution. Following the jitter screen, the next trial began.

Once all runs were completed, participants were randomly assigned one of the trials for which they were paid by rolling dice. If the randomly selected trial was a Person treatment, then participant was paid based on the payoff matrix and both players' decisions. If the trial was a Lottery treatment, the participant rolled a die to determine which of the two outcomes they received.

2.3. Behavioral analysis

We estimate the effect of the treatments on the probability of choosing payoff dominant. We used a logit model with the participants as random effects. The two factors plus an interaction term were encoded as dummy variables. A matrix-reward index was included to capture matrix-specific incentives.

The matrix-reward index is a modified Nash product for a normal form game: $((A - C)/(B - D))$ where A, B, C, and D are the payoffs in the game matrix (see Fig. 1A). Since there were no payoffs for the other player in the lottery treatments, we removed the elements of the equation that were part of the other player's payoffs. The index reflects the relative range in the reward of risk and payoff dominant choices. The modified Nash product index was chosen due to its explanatory power in predicting participant behavior compared to alternative matrix-reward indexes.

² Standard 4-button box.

2.4. fMRI data acquisition and analysis

Functional imaging was performed with a Siemens 3 T Trio whole-body scanner. T1-weighted structural images (TR = 2600 ms, TE = 3.02 ms, flip angle = 8°, 240 × 256 matrix, 176 sagittal slices, 1 mm³ voxel size) were acquired for each subject prior to the four experimental runs. For each experimental run, T2*-weighted images using an echo-planar imaging sequence were acquired, which show blood oxygen level-dependent (BOLD) responses (echo-planar imaging, TR = 2000 ms, TE = 30 ms, flip angle = 73°, FOV = 192 mm × 192 mm, 64 × 64 matrix, 33 3.5-mm thick axial slices, and 3 × 3 × 3.5 mm voxels).

fMRI data was analyzed using SPM8 (Wellcome Department of Imaging Neuroscience, University College London) with a two stage random-effects regression model. The data was subjected to standard preprocessing, including motion correction, slice timing correction, normalization to an MNI template brain, and smoothing using an isotropic Gaussian kernel (full-width half-maximum = 8 mm). A standard 2-stage random-effects GLM using a parametric hemodynamic response function (HRF) was used for statistical inference.

We designed a GLM with trial regressors for each of the four treatments. To account for differences in expected rewards, we separated each treatment into payoff dominant and risk dominant responses, which doubles the trial regressors. The HRF in the 8 trial regressors were parametrically modulated by the matrix-reward index. The modulator controls for reward differences between game matrices by absorbing BOLD signals related to the range of the rewards in each matrix, which were unrelated to the treatment. Due to the mean centering of the modulator, we set an upper limit of the payoff index to 6, which brought the mean of the modulator closer to the median (see Appendix).

Each trial began when the participant was shown the game matrix and ended when they completed their decision. Task regressors were convolved with a standard canonical hemodynamic response function. Six motion regressors were added to compensate for participant movement: 3 position and 3 rotation variables. The task regressors, modulated regressors, and motion variables along with a constant were generated for each run.

Statistical thresholds for whole brain analysis were determined based on the smoothness of the second-level contrasts. We used AlphaSim, to estimate the combination of height and extent thresholds that yielded a whole-brain FWE < 0.05 (Ward, 2013). To do this, we used 3dFWHMx to estimate image smoothness from the square root of the masked SPM-generated residual (ResMS) image. We then used AlphaSim with a voxel-level threshold of $p < 0.005$ to find the cluster threshold at which the whole-brain FWE would be < 0.05, and which ranged from 41 to 124 voxels, depending on the specific contrast.

To test the hypothesis that ToM regions underlie the difference between strategic uncertainty and risk, we used anatomical ROIs for the following regions: ACC, PCC, STS, temporal poles, mPFC, fusiform gyrus, right TPJ and LPFC. We also examined the ROIs of the ventral striatum (VS) and the ventral medial prefrontal cortex (VMPFC) as a check if behavioral differences between participants were related to utility. All regions were defined with the Wake Forest University pickatlas and supplementary packages (Tzourio-Mazoyer et al., 2002; Maldjian et al., 2003, 2004). We calculated the ROIs using SPM, which implements an eigenvariate method.

Activations within the ROIs were checked for correlation with a participant's propensity to choose the payoff dominant choice. Pearson's estimates were used to establish the correlation between the percent signal change in the ROI and the number of payoff dominant choices made by the participant. We examined the percent signal change in the ROIs for both payoff dominant and risk dominant decision. All significance thresholds were corrected for multiple comparisons using Bonferroni ($n = 10$).

3. Results

Reaction times varied across participants but did not correlate with behavior. None of the reaction times in the four treatments were significantly different from the others (Appendix: Table 2). Average reaction times for all treatments were slightly longer than 10 s (avg = 10.24 s, se = 2.10 s). The average run lasted just over 15 min (avg = 909.68 s, se = 64.08 s).

Participants in our experiment chose a mixture of payoff and risk dominant. Participants, on average, chose payoff dominant 41/56 when playing a stag hunt game with a person with full information (PxP). There was considerable variation among participants with the lowest number of payoff dominant decision of 15/56 and the most at 54/56. Removing the information of the other player's payoffs reduced the average number of payoff dominant choices from 41/56 to 23/56, a significant difference (paired t -test, $t = 7.30$, $sd = 12.23$, $p < 0.001$, $df = 29$). Similarly, changing from a stag-hunt game with a person to a lottery significantly reduced the number of payoff dominant choices to 24/56 (paired t -test, $t = 5.85$, $sd = 16.10$, $p < 0.001$, $df = 29$). There were no significant differences between either of the lottery treatments or those of the missing information treatments (Fig. 2).

Logit regressions supported the tabulated findings. Neither the Person nor the Lottery treatment variables were significant in the model, while the interaction of the two factors was significant ($p < 0.001$) and positive (Table 1). Moreover, when logits were performed on just those treatments with full information, the Person treatment was both significant ($p < 0.001$) and positive, while when only missing information observations were used, the Person treatment was insignificant and negative. The matrix-reward index was significant ($p < 0.001$) and positive for all logits models.

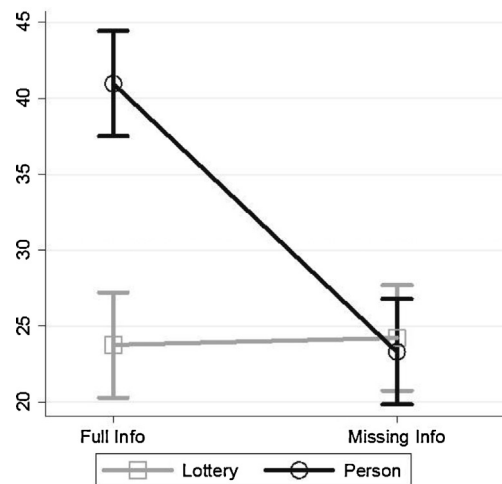


Fig. 2. (Above) Plot of the number of payoff dominant decisions chosen by each participant by treatment with 95% confidence interval error bars. Sample size is 30 participants. Paired *t*-test shows that LxF, PxM, and LxM treatments are not statistically different. PxM treatment is statistically different from all others ($p < 0.001$). (Right) A table of the tabulated data for each participant by treatment. The median number of payoff dominant are 43.5, 24, 26, and 23.5 for the PxM, PxM, LxF, and LxM treatments respectively.

Table 1

Random-effects logit regression of payoff dominant choice.

Variable	(1) Payoff dominant	(2) Payoff dominant	(3) Payoff dominant (Full Info)	(4) Payoff dominant (Missing Info)
Person	−0.070 (0.072)	−0.065 (0.075)	1.478*** (0.080)	−0.064 (0.076)
Full	−0.036 (0.072)	−0.015 (0.075)		
Person*full	1.467*** (0.105)	1.532*** (0.109)		
Matrix index		−0.033*** (0.003)	−0.029*** (0.004)	−0.039*** (0.005)
Constant	−0.296*** (0.113)	−0.385*** (0.122)	−0.415*** (0.131)	−0.380*** (0.127)
Observations	6720	6506	3262	3244
Number of sub	30	30	30	30

Legend: Table of regression coefficients for random-effects logit. Treatment regressors and interaction term were coded as dummy variables. Matrix index was a continuous variable. Note that when only full information observations are used, the person vs. lottery factor is significant ($p < 0.001$) and positive, but when only missing information observations were used, the person vs. lottery factor is insignificant and negative. Matrix index reduces number of observations due to the logit function. Standard errors in parentheses.

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

3.1. Imaging results

As a baseline, we contrasted images acquired while making a payoff dominant decision with those acquired while making a risk dominant decision for each treatment (Tables 2–5). In both the Person treatments, we found greater activation in the parietal lobe when a payoff dominant decision is made versus a risk dominant decision, which several studies also found during ToM tasks (Calarge et al., 2003; Mitchell et al., 2005; Sommer et al., 2007). The parietal lobe was also found in LxM treatment for payoff dominant decision, which suggests that the parietal lobe may be encoding some aspect of the payoff dominant choice and not necessarily the presence of another player. Risk dominant decisions showed greater activity in the insula compared to payoff dominant decisions during the PxM and LxF treatments. Several studies have suggested that the insula is a region involved in risk and ambiguity processing (Kuhnen and Knutson, 2005; Preuschoff et al., 2008; Xue et al., 2010). The increased activation in the insula during the risk dominant decisions for both Person and Lottery treatments supports the theory that the risk dominant decision is chosen as a way to reduce risk.

The behavioral data suggests that there is no significant behavioral difference between LxF and LxM, or PxM and LxM. As such, we restricted our neuroimaging analysis to the contrasts where behavioral differences underpin the differences in the neuroimages.³ We assume that participants who made the same number of payoff dominant/higher risk decisions in

³ Contrast tables for LxF vs. LxM and PxM vs. LxM are in the appendix.

Table 2
Risk and payoff dominant choice contrasts for treatment PxF.

Structure	L/R/B	Voxels	Peak voxel (MNI)			Max <i>t</i>
			X	Y	Z	
<i>PxF (payoff dom. trials > risk dom. trials)</i>						
Superior occipital	L	109	–27	–73	55	4.05
Superior occipital	R	162	33	–64	62	3.71
Middle occipital gyrus	R	315	33	–76	5	3.43
Middle occipital gyrus	L	123	–18	–88	–8	3.24
<i>PxF (risk dom. trials > payoff dom. trials)</i>						
No significant clusters						

Legend: Whole brain analysis of risk dominant and payoff dominant choice contrasts for each treatment. Significance thresholds set at $p < 0.005$ with a cluster threshold (k -value) set by AlphaSim such that FWE < 0.05 .

Table 3
Risk and payoff dominant choice contrasts for treatment PxM.

Structure	L/R/B	Voxels	Peak voxel (MNI)			Max <i>t</i>
			X	Y	Z	
<i>PxM (payoff dom. trials > risk dom. trials)</i>						
Middle frontal gyrus	R	116	30	17	59	4.71
Inferior parietal	L	93	–42	–64	55	3.27
Precuneus	B	71	6	–67	48	3.54
<i>PxM (risk dom. trials > payoff dom. trials)</i>						
Insula	L	107	–39	–4	24	4.44
Insula	R	170	15	–22	27	4.40
Medial frontal gyrus	L	124	–12	–22	62	3.45

Legend: Whole brain analysis of risk dominant and payoff dominant choice contrasts for each treatment. Significance thresholds set at $p < 0.005$ with a cluster threshold (k -value) set by AlphaSim such that FWE < 0.05 .

Table 4
Risk and payoff dominant choice contrasts for treatment LxF.

Structure	L/R/B	Voxels	Peak voxel (MNI)			Max <i>t</i>
			X	Y	Z	
<i>LxF (payoff dom. trials > risk dom. trials)</i>						
No significant clusters						
<i>LxF (risk dom. trials > payoff dom. trials)</i>						
Insula	R	93	30	–1	27	3.17

Legend: Whole brain analysis of risk dominant and payoff dominant choice contrasts for each treatment. Significance thresholds set at $p < 0.005$ with a cluster threshold (k -value) set by AlphaSim such that FWE < 0.05 .

Table 5
Risk and payoff dominant choice contrasts for treatment LxM.

Structure	L/R/B	Voxels	Peak voxel (MNI)			Max <i>t</i>
			X	Y	Z	
<i>LxM (payoff dom. trials > risk dom. trials)</i>						
Inferior parietal	R	80	54	–52	45	3.88
<i>LxM (risk dom. trials > payoff dom. trials)</i>						
No significant clusters						

Legend: Whole brain analysis of risk dominant and payoff dominant choice contrasts for each treatment. Significance thresholds set at $p < 0.005$ with a cluster threshold (k -value) set by AlphaSim such that FWE < 0.05 .

the LxF as those in the PxF perceived both the lottery and strategically uncertain game as posing similar amount of risk. Conversely, participants who made more payoff dominant/higher risk decisions in the PxM treatment than the LxF treatment likely viewed the presence of another person as a mitigating factor. Thus, the change in behavior is a metric for the extent to which participants differentiate between risk of a lottery and risk present in a strategically uncertain game.

When contrasting PxM with LxF, we found that presenting the other person's payoffs did not significantly increase brain activity in either the payoff dominant decisions or the risk dominant decisions (Table 6). Conversely, removing the other player's payoff increased brain activity in both the payoff dominant decisions and the risk dominant decisions. Risk dominant decisions showed increased activity in parietal lobe, cingulate, and dorsal lateral prefrontal cortex. These regions

Table 6
PxF and PxM contrasts.

Structure	L/R/B	Voxels	Peak voxel (MNI)			Max <i>t</i>
			X	Y	Z	
<i>Payoff dom. trials (PxF > PxM)</i>						
No significant clusters						
<i>Payoff dom. trials (PxM > PxF)</i>						
Precentral gyrus	L	136	−42	−13	59	3.61
Lingual gyrus	R	86	−9	−88	−8	3.1
<i>Risk dom. trials (PxF > PxM)</i>						
No significant clusters						
<i>Risk dom. trials (PxM > PxF)</i>						
Inferior parietal	L	126	−51	−22	20	5.69
Cingulate gyrus	L	353	−9	−4	55	5.27
Cuneus	B	2542	−6	−100	10	5.07
Postcentral gyrus	L	633	−30	−31	52	4.75
Medial frontal	L	83	−9	−37	69	4.5
Precentral gyrus	L	71	−39	−1	34	3.68
Superior parietal	L	75	−24	−70	45	3.46

Legend: Whole brain analysis of Person × Full and Person × Missing contrasts for both risk dominant and payoff dominant choices.

Table 7
PxF and LxF contrasts.

Structure	L/R/B	Voxels	Peak voxel (MNI)			Max <i>t</i>
			X	Y	Z	
<i>Payoff dom. trials (PxF > LxF)</i>						
Cuneus	L	323	−15	−100	−5	6.91
Cuneus	R	187	18	−94	−1	5.39
<i>Payoff dom. trials (LxF > PxF)</i>						
Middle temporal gyrus	L	200	−60	−58	−12	5.33
Middle temporal gyrus	R	82	48	−76	6	4.14
Cuneus	B	452	9	−88	20	5.15
<i>Risk dom. trials (PxF > LxF)</i>						
No significant clusters						
<i>Risk dom. trials (LxF > PxF)</i>						
Cuneus	B	1739	6	−91	17	6.47
Thalamus (pulvinar)	B	905	−6	−25	3	6.31
Medial frontal gyrus	B	607	0	29	52	5.9
Middle frontal gyrus (Precentral gyrus)	L	2284	−39	53	−5	5.5
Middle frontal gyrus	R	243	42	29	20	5.32
Middle frontal gyrus	R	329	54	14	45	4.17
Middle occipital gyrus	L	74	−42	−79	−1	4.2

Legend: Whole brain analysis of Person × Full and Lottery × Full contrasts for both risk dominant and payoff dominant choices. Both analyses use a significance thresholds set at $p < 0.005$ with a cluster threshold (k -value) set by AlphaSim such that FWE < 0.05 .

have been implicated in ToM tasks, but a meta-analysis by Krain et al. (2006) argues that these regions are likely involved with ambiguity. The ambiguity created from a reduction of information in our experiment seems to support this hypothesis.

In our anatomical ROI analysis, we found that none of activity in the ToM or utility regions correlated with the behavioral differences between PxF and PxM treatments (Table 8). The lack of behavioral correlation, along with the presence of regions involved in ambiguity, suggests that the behavioral differences observed between these treatments are from ambiguity and not differences in risk or strategic uncertainty.

When contrasting PxF with LxF, we found increased activity in the occipital lobe for both PxF and LxF when payoff dominant decisions are made (Table 7). The presence of the occipital lobe is likely reflecting the visual differences between the two treatments. Although the PxF treatment did not show an increase in the risk dominant choices, the LxF showed a considerable increase in PFC activity. Both ToM and risk tasks have found PFC activity, but the lottery treatment seem to use these region more intensively. It is likely that all interpersonal game decisions are inherently risky, but other circuits are also engaged to make the decision. On the other hand, lotteries are strictly risk related and must rely on utility circuits more heavily.

Three ToM regions were significantly correlated with behavioral differences between treatments (Table 9). Participants who chose payoff dominant more often in the PxF treatment than the LxF treatment also exhibited a greater percent signal change in the ACC, PCC, and fusiform ($r = 0.506$, $p < 0.05$; $r = 0.681$, $p < 0.001$; $r = 0.628$, $p < 0.001$; respectively) during the

Table 8
Correlations table Person × Full–Person × Missing.

Theroy of mind	PD	RD	Utility and risk
Anterior cingulate cortex (ACC)	–0.039	0.170	
Posterior cingulate cortex (PCC)	0.290	–0.070	
Superior temoairal sulcus (STS)	0.257	0.081	
Temporal poles	0.105	0.097	
Medial perfontal cortex (mPFC)	0.001	0.200	
Fusiform	0.331	–0.356	
Temporal parietal junction (TPJ)	0.096	0.158	
Lateral prefontal cortex (LPFC)	–0.011	–0.104	
	0.004	0.010	Ventral striatum
	0.009	0.148	Ventromedial prefrontal cortex (vmPFC)

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Legend: Table of correlations between the percentage signal change in an anatomical ROI and the change in payoff dominant decisions in the difference between Person × Full and Person × Missing treatments. Note that there are no significant correlations between participant's decisions and contrast signal change in any of the ROIs.

Table 9
Correlations table Person × Full–Lottery × Full.

Theroy of mind	PD	RD	Utility and risk
Anterior cingulate cortex (ACC)	0.506*	0.317	
Posterior cingulate cortex (PCC)	0.681***	–0.037	
Superior temoairal sulcus (STS)	0.430	0.308	
Temporal poles	0.335	0.299	
Medial perfontal cortex (mPFC)	0.300	0.314	
Fusiform	0.628***	–0.166	
temporal parietal junction (TPJ)	0.369	0.384	
Lateral prefontal cortex (LPFC)	0.339	0.238	
	0.098	0.246	Ventral striatum
	0.396	0.254	Ventromedial prefrontal cortex (vmPFC)

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Legend: Table of correlations between the percentage signal change in an anatomical ROI and the change in payoff dominant decisions in the difference between Person × Full and Lottery × Full treatments. Signal change of payoff dominant trial regressors (PD) and risk dominant trial regressors (RD) were considered separately due to observed differences between decision contrasts. Significance thresholds were corrected for multiple comparisons using Bonferroni's formula ($n = 10$). Anatomical ROI listed in columns of similar functionality.

payoff dominant choices (Fig. 3). For the risk dominant decisions, none of the ToM regions correlated with the differences in behavior. Thus, the ACC, PCC, and fusiform are correlated with the likelihood a participant would choose payoff dominant. None of the utility regions showed a significant correlation with behavior for either payoff or risk dominant decisions. The lack of a significant correlation in the utility regions of the brain suggests that behavioral differences between the Person and Lottery treatments are unlikely due to differences in perceived risk. As such, strategic uncertainty may use a separate mechanism, which helps support a cooperative solution.

4. Discussion

The present study seeks to understand the differences between strategic uncertainty and risk. The stag-hunt game is the quintessential example of strategic uncertainty while a choice between lotteries is the standard for inducing risk preferences. Our experiment compares these two tasks with similar financial incentives to test if strategic uncertainty is comparable to risk. We found that individuals are more likely to make a payoff dominant choice if playing a coordination game, a stag hunt, with a person than deciding between two lotteries with equivalent incentives. Participants in our study almost doubled the number of payoff dominant decisions in a stag hunt compared to a choice between lotteries. We found that the difference in the propensity to make a payoff dominant decision between a stag-hunt game and a choice between lotteries correlated with the percent signal change in an individual's ACC, PCC, and fusiform gyrus.

Past experiments have shown that the ACC responded to viewing the decisions of other players (Tomlin et al., 2006). An alternative explanation is that the ACC resolves conflict between multiple inputs (Aarts et al., 2008; Nee et al., 2011), such as a signal of utility and a signal of social reward. Thus, the ACC's correlations with behavior could be responding to increased conflict between signals as much as being involved with ToM.

The PCC and the fusiform gyrus had similar correlation with behavior and are located adjacent to one other in the brain. The fusiform, in particular the fusiform face area (FFA), has been identified as part of ToM circuit (Schultz et al., 2003; Dalton et al., 2005; Gobbini et al., 2011). In particular, the FFA has been shown to have reduced activity in patients with Autism Spectrum Disorder (ASD) who displayed a reduction in cooperative decision compared to a health control (Schultz et al., 2003). Similar to the fusiform, past studies of participants with ASD have also shown blunted activations in the PCC during an investment task, which requires one player to trust the other player (Chiu et al., 2008).

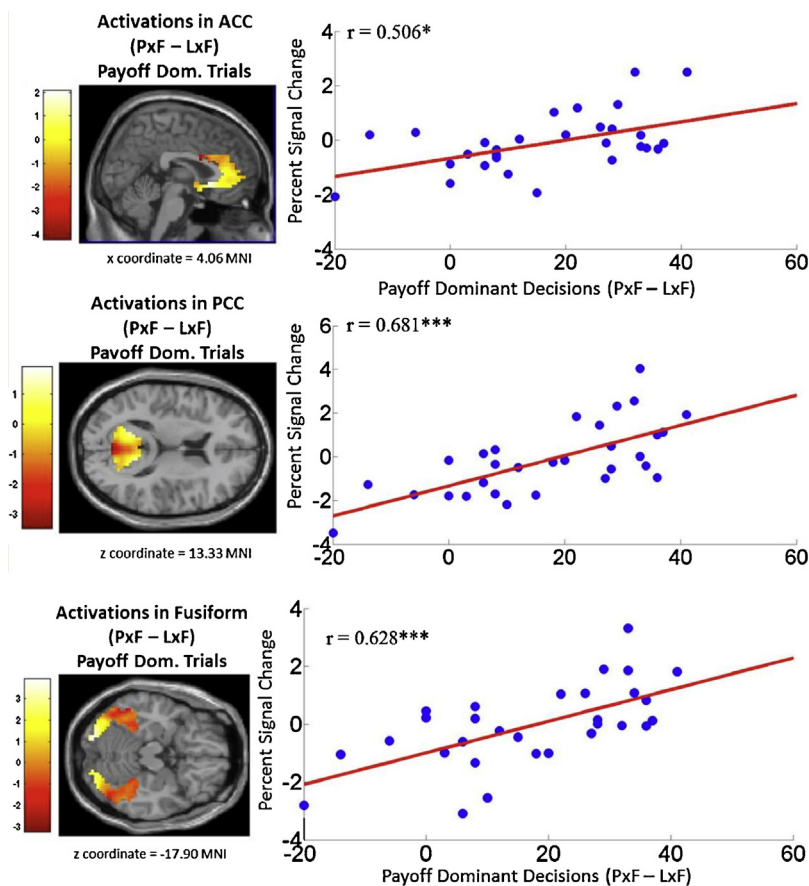


Fig. 3. (Above) Scatter plots of significant correlations in the ACC and the PCC. Brain maps, on the left, are anatomical inclusive masks for the contrast of Person \times Full > Lottery \times Full. Scatter plots, on the right, show correlations of the percent signal change and the change in payoff dominant decisions for the contrast. (Below) Scatter plots of fusiform correlations.

We also found that removing the information of the other player's payoffs reduced the payoff dominant decisions by half, but we found no discernible difference in payoff dominant choices when the probability of each outcome were removed from the lotteries. Neuroimaging contrasts between the Full and Missing information treatments of the stag hunt game showed greater activation in the insula during risk dominant decisions. The insula has been implicated in ambiguity aversion (Kuhnen and Knutson, 2005; Preuschhoff et al., 2008; Xue et al., 2010). Thus, the observed differences between the stag hunt game with full information and those with missing information are likely ambiguity.

The increased activity in the ToM regions and no discernible differences in the utility regions of the brain suggest that strategic uncertainty is evoking a separate circuit than that of risk. It is likely that both risk and strategic uncertainty are employing circuits for evaluating random events, but the strategically uncertain games generate an additional input due to the presence of the other player. The extent to which an individual believes they are interacting with an individual may determine the likelihood they will choose a cooperative strategy. The correlation between the activity in the ToM regions and the propensity to choose payoff dominant may be a manifestation of these beliefs. Thus, we argue that the differences between game theoretic predictions and observed behavior in coordination games is not inaccuracy in predicting randomization, but differences in perceived models by the individual.

There is still a debate over which regions are specialized for mentalizing another person. Some regions commonly associated with ToM are also implicated in other aspects of decision making; such as the mPFC and ACC are also associated with complex cognitive processing (Kerns, 2006; Koehlin and Summerfield, 2007; Kouneiher et al., 2009). Our study controlled for the complexity of cognitive processing by matching strategically uncertain games with a choice between equivalent lotteries. Our work supports the arguments that the cingulate cortex has a primary role in ToM.

The feature that separates strategic uncertainty from risk is the involvement of another person. Thus, generating a mental model of the other player is a prerequisite for choosing a strategy. For the bulk of human evolution, human interaction took place face-to-face. It was not until widespread literacy that human interactions could take place without another person present. If the recognition of a human player is a prerequisite to employing specialized circuits for facilitating human interaction, then regions that specialize in facial recognition must have coevolved with regions for modeling another person.

As such, the fusiform as a switch, due to the FFA, and the PCC as a region where the model is generated are good candidates for the ToM circuit.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.jebo.2013.07.006>.

References

- Aarts, E., Roelofs, A., van Turenout, M., 2008. Anticipatory activity in anterior cingulate cortex can be independent of conflict and error likelihood. *Journal of Neuroscience* 28 (April (18)), 4671–4678.
- Abler, B., Walter, H., Erk, S., Kammerer, H., Spitzer, M., 2006. Prediction error as a linear function of reward probability is coded in human nucleus accumbens. *NeuroImage* 31 (June (2)), 790–795.
- Aumann, R.J., 1987. Correlated equilibrium as an expression of bayesian rationality. *Econometrica* 55 (1), 1–18.
- Baron-Cohen, S., 1989. The autistic child's theory of mind: a case of specific developmental delay. *Journal of Child Psychology and Psychiatry* 30 (March (2)), 285–297.
- Battalio, R., Samuelson, L., Van Huyck, J., 2001. Optimization incentives and coordination failure in laboratory stag hunt games. *Econometrica* 69 (May (3)), 749–764.
- Breiter, H.C., Aharon, I., Kahneman, D., Dale, A., Shizgal, P., 2001. Functional imaging of neural responses to expectancy and experience of monetary gains and losses. *Neuron* 30 (May (2)), 619–639.
- Calarge, C., Andreasen, N.C., O'Leary, D.S., 2003. Visualizing how one brain understands another: a pet study of theory of mind. *American Journal of Psychiatry* 160 (11), 1954–1964.
- Carrington, S.J., Bailey, A.J., 2009. Are there theory of mind regions in the brain? A review of the neuroimaging literature. *Human Brain Mapping* 30 (August (8)), 2313–2335.
- Chiu, P.H., Kayali, M.A., Kishida, K.T., Tomlin, D., Klinger, L.G., Klinger, M.R., Montague, P.R., 2008. Self responses along cingulate cortex reveal quantitative neural phenotype for high-functioning autism. *Neuron* 57 (3), 463–473.
- Corcoran, R., Mercer, G., Frith, C.D., 1995. Schizophrenia, symptomatology and social inference: investigating 'theory of mind' in people with schizophrenia. *Schizophrenia Research* 17 (September (1)), 5–13.
- Dalton, K.M., Nacewicz, B.M., Johnstone, T., Schaefer, H.S., Gernsbacher, M.A., Goldsmith, H.H., Alexander, A.L., Davidson, R.J., 2005. Gaze fixation and the neural circuitry of face processing in autism. *Nature Neuroscience* 8 (April (4)), 519–526.
- Dreher, J.-C., Kohn, P., Berman, K.F., 2006. Neural coding of distinct statistical properties of reward information in humans. *Cerebral Cortex* 16 (April (4)), 561–573.
- Fellows, L.K., Farah, M.J., 2007. The role of ventromedial prefrontal cortex in decision making: judgment under uncertainty or judgment per se? *Cerebral Cortex* 17 (November (11)), 2669–2674.
- Gobbini, M.I., Gentili, C., Ricciardi, E., Bellucci, C., Salvini, P., Laschi, C., Guazzelli, M., Pietrini, P., 2011. Distinct neural systems involved in agency and animacy detection. *Journal of Cognitive Neuroscience* 23 (December (8)), 1911–1920.
- Hare, T.A., Camerer, C.F., Rangel, A., 2009. Self-control in decision-making involves modulation of the vmPFC valuation system. *Science* 324 (May (5927)), 646–648.
- Harsanyi, J.C., Selten, R., 1988. *A General Theory of Equilibrium Selection in Games*, vol. 1. MIT Press Books, The MIT Press.
- Huyck, J.B.V., Battalio, R.C., Beil, R.O., 1990. Tacit coordination games, strategic uncertainty, and coordination failure. *The American Economic Review* 80 (1), 234–248.
- Kable, J.W., Glimcher, P.W., 2007. The neural correlates of subjective value during intertemporal choice. *Nature Neuroscience* 10 (December (12)), 1625–1633.
- Kerns, J.G., 2006. Anterior cingulate and prefrontal cortex activity in an fMRI study of trial-to-trial adjustments on the simon task. *NeuroImage* 33 (October (1)), 399–405.
- Knutson, B., Adams, C.M., Fong, G.W., Hommer, D., 2001. Anticipation of increasing monetary reward selectively recruits nucleus accumbens. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience* 21 (August (16)), RC159.
- Koechlin, E., Summerfield, C., 2007. An information theoretical approach to prefrontal executive function. *Trends in Cognitive Sciences* 11 (June (6)), 229–235.
- Kouneither, F., Charron, S., Etienne, K., 2009. Motivation and cognitive control in the human prefrontal cortex. *Nature Neuroscience* 12 (July (7)), 939–945.
- Krain, A.L., Wilson, A.M., Arbuckle, R., Castellanos, F.X., Milham, M.P., 2006. Distinct neural mechanisms of risk and ambiguity: a meta-analysis of decision-making. *NeuroImage* 32 (1), 477–484.
- Kuhnen, C.M., Knutson, B., 2005. The neural basis of financial risk taking. *Neuron* 47 (September (5)), 763–770.
- Maldjian, J.A., Laurienti, P.J., Burdette, J.H., 2004. Precentral gyrus discrepancy in electronic versions of the Talairach atlas. *NeuroImage* 21 (1), 450–455.
- Maldjian, J.A., Laurienti, P.J., Kraft, R.A., Burdette, J.H., 2003. An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *NeuroImage* 19 (3), 1233–1239.
- McClure, S.M., Nathaniel, D., Daw, P., Montague, R., 2003. A computational substrate for incentive salience. *Trends in Neurosciences* 26 (August (8)), 423–428.
- Mitchell, J.P., Banaji, M.R., Macrae, C.N., 2005. The link between social cognition and self-referential thought in the medial prefrontal cortex. *Journal of Cognitive Neuroscience* 17 (8), 1306–1315.
- Nee, D.E., Kastner, S., Brown, J.W., 2011. Functional heterogeneity of conflict, error, task-switching, and unexpectedness effects within medial prefrontal cortex. *NeuroImage* 54 (January (1)), 528–540.
- O'Doherty, J., Dayan, P., Schultz, J., Deichmann, R., Friston, K., Dolan, R.J., 2004. Dissociable roles of ventral and dorsal striatum in instrumental conditioning. *Science* 304 (April (5669)), 452–454.
- Pagnoni, G., Caroline, F., Zink, P., Montague, R., Berns, G.S., 2002. Activity in human ventral striatum locked to errors of reward prediction. *Nature Neuroscience* 5 (February (2)), 97–98.
- Preuschhoff, K., Quartz, S.R., Bossaerts, P., 2008. Human insula activation reflects risk prediction errors as well as risk. *The Journal of Neuroscience* 28 (March (11)), 2745–2752.
- Radner, R., Rosenthal, R.W., 1982. Private information and pure-strategy equilibria. *Mathematics of Operations Research* 7 (3), 401–409.

- Ramnani, N., Owen, A.M., 2004. Anterior prefrontal cortex: insights into function from anatomy and neuroimaging. *Nature Reviews Neuroscience* 5 (March (3)), 184–194.
- Rankin, F.W., Van Huyck, J.B., Battalio, R.C., 2000. Strategic similarity and emergent conventions: evidence from similar stag hunt games. *Games and Economic Behavior* 32 (2), 315–337.
- Rubinstein, A., 1991. Comments on the interpretation of game theory. *Econometrica* 59 (4), 909–924.
- Schultz, R. T., Grelotti, D.J., Klin, A., Kleinman, J., Van der Gaag, C., Marois, R., Skudlarski, P., 2003. The role of the fusiform face area in social cognition: implications for the pathobiology of autism. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 358 (February (1430)), 415–427.
- Skyrms, B., 2001. The Stag Hunt. *Proceedings and Addresses of the American Philosophical Association* 75 (November (2)), 31–41.
- Sommer, M., Döhl, K., Sodian, B., Meinhardt, J., Thoermer, C., Hajak, G., 2007. Neural correlates of true and false belief reasoning. *NeuroImage* 35 (3), 1378–1384.
- Straub, P.G., 1995. Risk dominance and coordination failures in static games. *The Quarterly Review of Economics and Finance* 35 (4), 339–363.
- Tomlin, D.M., Kayali, A., King-Casas, B., Anen, C., Camerer, C.F., Quartz, S.R., Read Montague, P., 2006. Agent-specific responses in the cingulate cortex during economic exchanges. *Science* 312 (May (5776)), 1047–1050.
- Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., Mazoyer, B., Joliot, M., 2002. Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *NeuroImage* 15 (1), 273–289.
- Ward, B.D., 2013. AlphaSim. <http://afni.nimh.nih.gov/>
- Xue, G., Lu, Z., Levin, I.P., Bechara, A., 2010. The impact of prior risk experiences on subsequent risky decision-making: the role of the insula. *NeuroImage* 50 (April (2)), 709–716.