

Neurocomputational mechanisms engaged in detecting cooperative and competitive intentions of others

Rémi Philippe, Rémi Janet, Koosha Khalvati, Rajesh P N Rao, Daeyeol Lee, Jean-Claude C Dreher

▶ To cite this version:

Rémi Philippe, Rémi Janet, Koosha Khalvati, Rajesh P N Rao, Daeyeol Lee, et al.. Neurocomputational mechanisms engaged in detecting cooperative and competitive intentions of others. 2022. hal-03855508

HAL Id: hal-03855508 https://cnrs.hal.science/hal-03855508

Preprint submitted on 16 Nov 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Neurocomputational mechanisms engaged in detecting cooperative and competitive intentions of others

Rémi Philippe

CNRS - Institut des Sciences Cognitives Marc Jeannerod https://orcid.org/0000-0003-2894-7688

Rémi Janet

CNRS, Institut des Sciences Cognitives Marc Jeannerod

Koosha Khalvati

Paul G. Allen School of Computer Science and Engineering, University of Washington

Rajesh Rao

University of Washington

Daeyeol Lee

Johns Hopkins University https://orcid.org/0000-0003-3474-019X

Jean-Claude Dreher (☐ dreher@isc.cnrs.fr)

CNRS, Institut des Sciences Cognitives Marc Jeannerod https://orcid.org/0000-0002-2157-1529

Article

Keywords:

Posted Date: January 18th, 2022

DOI: https://doi.org/10.21203/rs.3.rs-1160167/v1

License: © (i) This work is licensed under a Creative Commons Attribution 4.0 International License.

Read Full License

Neurocomputational mechanisms engaged in detecting cooperative and competitive intentions of others

R. Philippe ¹, R. Janet ¹, K Khalvati ², R.P.N. Rao ^{2,3}, D Lee⁴, JC. Dreher ^{1*}

- ¹ CNRS-Institut des Sciences Cognitives Marc Jeannerod, UMR5229, Neuroeconomics, reward, and decision making laboratory. 67 Bd Pinel, 69675 Lyon, FRANCE
- ² Paul G. Allen School of Computer Science and Engineering, University of Washington, 185 Stevens
- ³ Center for Neurotechnology, University of Washington, Seattle, WA 98195
- ⁴ The Zanvyl Krieger Mind/Brain Institute, Kavli Neuroscience Discovery Institute, Department of
- Neuroscience, Department of Psychological and Brain Sciences, Johns Hopkins University, 3400 N.
- Charles St. Baltimore, MD 21218, USA

* Corresponding author

Abstract

Humans frequently interact with other agents whose intentions can fluctuate over time between competitive and cooperative strategies. How does the brain decide whether the others' intentions are to cooperate or compete when the nature of the interactions is not explicitly signaled? We used model-based fMRI and a task in which participants thought they were playing with another player. In fact, this agent was an algorithm alternating without signaling between cooperative and competitive strategies. A neurocomputational mechanism underlying arbitration between competitive and cooperative experts outperforms other learning models in predicting choice behavior. The ventral striatum and ventromedial prefrontal cortex tracked the reliability of this arbitration process. When attributing competitive intentions, these regions increased their coupling with a network that distinguish prediction error related to competition *versus* cooperation. These findings provide a neurocomputational account of how the brain dynamically arbitrates between cooperative and competitive intentions when making adaptive social decisions.

Introduction

43

44

45

46

47

48

49

50

51

52

53

54

55

56

57

58 59

60 61

62

63

64

65

66

67

68

69

70

71

72

73 74

75

76

77

78

During social interactions, humans are often uncertain whether others intend to compete or cooperate. The intentions of other agents can fluctuate over time, making it challenging to develop behavioral strategies. A key question is to understand how the brain decides whether the other is cooperating or competing during volatile situations in which the nature of the social interactions is not explicitly determined, as when others interact to achieve a common goal while maximizing their own benefits. This question is of importance since it lies at the heart of strategic social decision making 1-9. In these types of situations, other agents can change behavior according to cooperative or competitive intentions. Cooperation is generally defined as involving a group of individuals working together to attain a common goal ^{10,11}. In contrast, competition involves one person attempting to outperform another in a zero-sum situation ¹². A number of theoretical accounts and experimental results demonstrate that the ability to mentalize, i.e. to simulate the other's belief about one's next course of action, is crucial for strategically sophisticated agents ^{6,7,13,14}. The neurocomputational mechanisms engaged in attributing intentions to others has been studied in situations in which participants are explicitly informed about the nature of the interactions, either in a collaborative context alone ^{15–17} or in a competitive context alone 8,18-25. For example, during a cooperative game such as the coordination game, one of the best strategies is to try to choose one of two presented targets consistently. In contrast, in a competitive game such as the matching pennies game ^{19,25}, the optimal strategy is to choose between two targets equally often and randomly across trials. If the identity of the game played is not known, the agent has adjust his/her strategy based on repeated interactions with others and to infer cooperation/competition on the basis of observations. How the brain achieves such inference poses a unique computational problem because it not only requires the recursive representation of reciprocal beliefs about other's intentions, as in cooperative or competitive contexts alone, but it also requires one to decide whether the other is competing or cooperating to deploy an appropriate behavioral strategy.

Here, we sought to determine the neurocomputational mechanisms that underlie the inferences of whether a person is competing or cooperating during volatile situations in which the nature of the interactions is not explicitly signaled. A recent computational account proposed that arbitration between strategies is determined by their predictive reliability, such that control over behavior is adaptively weighted toward the strategy with the most reliable prediction ²⁶. This approach has been tested successfully in the domains of instrumental or Pavlovian action selection ²⁷, model-based and model-free learning ²⁸ and learning by imitation or emulation ²⁹. Extending this concept of a mixture of experts to social interactions, we investigated whether the brain relies on distinct experts to compute the best choice between two possible intentions attributed to others (cooperation or competition) and then weights them by their relative reliability. We tested and compared these mixtures of models, that attribute intentions to others dynamically, with different classes of learning models: non-Bayesian vs Bayesian and non-mentalizing vs mentalizing (see table 1). This allowed us to identify the algorithms

and brain mechanisms engaged with a key component of the estimation of other's intentions, i.e. whether the social partner was cooperating or competing.

The majority of theoretical frameworks used to model feedback-dependent changes in decision making strategies, such as choice reinforcement and related Markov Decision Process (MDP) models, assume that optimal decisions can be determined from the observable events and variables by the decision makers. Clearly, these assumptions do not capture the reality and complexity of human social interactions because observable behaviors of other individuals provide only very partial information about their likely future behaviors. Moreover, model-free RL algorithms assume that values (utility or desirability of states and actions), change incrementally across trials. This assumption is incorrect when option values change abruptly, such as when the intention of the other shifts between cooperation and competition. These limitations explain why agents basing their behavior only on standard RL models can be exploited by opponents using more sophisticated algorithms ^{6,30}.

A more accurate account of strategic learning is based on a family of RL models which adds a mathematical term to the classical Temporal Difference (TD) algorithm to consider the other as an agent having their own policy, which can be influenced by oneself ^{6,30,31}. For example, fictitious play learning proposes a basic form of mentalizing by having a representation of the other's strategy. Influence models also consider that RL can be supplemented by a mentalizing term that represents how our actions influence those of others, updated through a belief prediction error ^{2,6,19,21,30,32–34}. Such influence models formalize not only how players react to others' past choices, (first-order beliefs in Theory of Mind: ToM), but also how they anticipate the influence of their own choices on the others' behavior (i.e., mentalizing-related second-order beliefs). Another modeling approach of theory of mind used Bayesian algorithms to model inferences about the future actions of another, attempting to take their point of view and to simulate their decision ^{13,17,35}. This strategy can be performed recursively so that participants make inferences concerning the others' inferences and so on. Such a sophisticated approach could be grounded in the theoretical framework of Partially Observable Markov Decision Processes (POMDPs) ³⁶. POMDPs provide a probabilistic framework for solving tasks involving action selection and decision making under uncertainty ^{37,38}. Notably, this approach has recently been applied to strategic cooperation in groups ^{36,39,40}. These models, however, have mainly been limited to signaled cooperative or competitive tasks where the intentions of players do not change over a given period 13,35,41,42.

Here, we tested the predictions of these different families of learning models against one another, investigating not only non-Bayesian vs Bayesian models and non-mentalizing vs mentalizing models, but also a mixture of models deploying an arbitration process whereby the influence of attributing intentions to others is dynamically modulated depending on which type of intention (i.e. cooperative vs competitive) is most suitable to guide behavior at a given time. We did so by using a novel model-based fMRI design (**Fig. 1**) consisting of an iterative dyadic game in which participants were told that they would interact with another person via a computer. Unbeknownst to them, the other

player was an artificial agent that switched between blocks of cooperative trials and blocks of competitive trials when playing a card matching game. Thus, the algorithm's goals were the same as those of participants in the Cooperative blocks but were orthogonal in Competitive blocks. Participants remained uncertain with respect to the goals of their "partner" or "opponent", which alternated, without being signaled. This task allowed us to investigate the algorithms used by the brain to recognize the "intentions" of others and to adopt appropriate strategies when the modes of interaction (cooperation vs competition) are not indicated.

115

116

117

118

119

120

121

122

123

124

125

126

127

128

129

130

131

132

133

134

135

136

137

138

139

140

141

142

We found that the model accounting best for behavior was a mixture of influence models. referred to as Mixed-Intention Influence Model. Two expert systems work together to make strategic decisions, one assessing competitive intentions and the other assessing cooperative intentions, a controller weighting between these experts according to their relative reliabilities. Each expert system uses a classic RL algorithm complemented with a mentalizing term to infer the other's actions. This Mixed-Intention Influence model accounts for behavior observed in naturalistic environments in which the other's goal is often only partially congruent with one's own, allowing for a continuous range of behavior between pure cooperation and pure competition. A brain network including the ventromedial prefrontal cortex (vmPFC) and the ventral striatum tracked the reliability signal from the controller. This finding indicates that the Mixed-Intention Influence model captures the higher-order structure of the mixed-intentions task (i.e., alternation between cooperation and competition). When comparing trials classified as competitive versus cooperative by the controller, we also identified a brain system engaged with an updating signal used for learning. Finally, when participants expected higher utility for choosing according to a competitive rather than cooperative strategies, the vmPFC and the ventral striatum, tracked the intentions of others and showed changes in functional connectivity with a brain system including the right temporo-parietal junction (rTPJ), dorsolateral prefrontal cortex (dIPFC) and the intraparietal sulcus (IPS), which discriminates reward prediction error (PE) between believed modes of interaction. Together, these results provide a model-based account of the neurocomputational mechanisms guiding human strategic decisions during games in which the intentions of others fluctuate between cooperation and competition.

Results

Behavioral signature of tracking intentions

We used logistic regression to examine whether participants selected the same target as that from the previous trial ("Stay") or chose the other target ("Switch"), depending on whether the previous three trials (at t-1, t-2 and t-3) had been won or lost, whether the previous decisions had been to Stay or Switch, and whether the previous interactions from those trials indicated cooperation (see below). We also added sex, age and the number of trials as control variables. All trials except the 5 initialization trials were included in this analysis. Cooperation was defined by a binomial variable, representing the interaction between the last action of the Artificial Agent (AA) and the participant's own previous outcome ("Cooperativity signature"). This variable was set to 1 if either the participant had won on the previous trial and the AA stayed on the same target for the next trial, or if the participant lost on the previous trial and the AA switched to the other target the trial just after. Otherwise, the variable was set to 0. Indeed, from the perspective of the participant, if the AA is a cooperative partner, both players win at the same time and should then choose to keep the same target to be more predictable.

We found that the "Cooperativity signature" predicted an increase in the "stay" probability of participants at t-1 and t-2 (Cooperativity signature $_{t-1}$: estimate = 0.05, p=0.021; Cooperativity signature $_{t-2}$: estimate = 0.05, p=0.002, χ^2 test **Fig. 2a**). This suggests the participants tracked whether the other agent was cooperating during the two previous trials (but not before). Participants used the outcome of the latest trial to make the next decision (staying or switching target) according to a win/stay, lose/switch strategy (winning_{t-1}: estimate = 0.16, p<0.0005, χ^2 test **Fig. 2a**).

Computational models tracking intentions of the other agent

To elucidate the computations underlying strategic decision making, we compared the results of different computational models. These models were split into five classes (**see SI**). The first class of models, based on heuristics, included Win-Stay/Lose-Switch and Random Bias models. The other four classes of algorithms can be classified into non-Bayesian *versus* Bayesian model families along one dimension and mentalizing versus non-mentalizing model families along the other dimension. Thus, the second class of models includes non-Bayesian, non-mentalizing models represented by reinforcement learning (RL) models. The third class represents non-Bayesian mentalizing models, namely the "influence models" which are RL models with an additional term representing how the actions of one player influence those of the other player. The fourth class corresponds to Bayesian non-mentalizing models, including (1) a Hierarchical Gaussian Filter (HGF) which tracks the volatility of outcome 43 , (2) the k-Bayesian Sequence Learner which tracks the probability that one target will be selected by the AA after a history of specific length k and (3) the *active inference* model which minimizes the expected

free energy ⁴⁴. The fifth class of models contains Bayesian mentalizing models, which are the *k*-ToM models using recursive Bayesian inferences of depth *k* to predict the future choice of the AA. Each mentalizing model was tested using 3 versions: a competitive, a cooperative and a 'mixed intentions' version. The 'mixed intentions' version computes one decision value according to a competitive expert and another according to a cooperative expert and arbitrates between the two, based on the difference in their respective reliability (**see SI, Fig. 3a**). We defined reliability as the difference in unsigned value functions for two choices given by particular learning algorithms.

178

179

180

181

182

183

184

185

186

187

188

189

190

191

192

193

194

195

196

197

198

199

200

201

202

203204

205

206

207

208

209

210211

212

213

Next, we performed a group-level random-effect Bayesian model selection on the models' computed free energy, taking into account potential outliers and the number of free parameters 45,46. We found that the 'Mixed Intentions Influence Learning' Model was the most frequent best fit across the population (Fig. 2b), demonstrating that subjects employed mentalizing-related computations in our mixed intentions task. This finding also indicates that arbitration between a cooperative and a competitive expert best explains most participants' behavior, rather than either expert taken individually. Additionally, only the Mixed-Intention Influence model (and not the cooperative or the competitive one) succeeded in producing behavior, similar to participants, with respect to the effect of the Cooperativity signature on the probability to stay (Fig. 3b and Extended Fig.1, see SI). We conducted a logistic regression to understand how the Mixed-Intention Influence model explained differences in behavioral strategy to stay or switch target. This analysis included the reward prediction error at t-1, the valence of the arbitration between cooperative and competitive intention at time t (sign(Δ); 1 for cooperative and -1 for competitive), and the interaction between these two variables. This analysis revealed a main effect of the valence of the arbitration (valence of the arbitration_t: estimate = 0.24, p < 0.0005, χ^2 test Fig. 3c) indicating that participant tend to stay more on the same target when they attributed cooperative intention to the other. Moreover, we found an interaction effect, i.e. participants did not integrate the prediction error in their strategy in the same way given the attributed intention (valence of the arbitration, * rPE_{t-1} : estimate = 0.20, p = 0.0227, χ^2 test **Fig. 3c**). That is, higher negative prediction errors increased the probability that the participant would stay on the same target when the controller attributed cooperative intentions compared to when it attributed competitive intentions. In addition, we also performed another logistic regression analysis using the same variables and the actual mode of interaction (i.e. competitive block trials versus cooperative block trials), rather than the classified mode of interaction made by the controller. We did not find the same interaction effect when we compared actual competitive and cooperative block trials (Block type, * rPE_{t-1} : estimate = 0.003, p = 0.56, Block type_t: estimate = 0.03, p = 0.229, and PE_{t-1} : estimate = $0.14, p < 0.0005, \chi^2$ test; **Extended Fig.2, see SI**), showing that the classified intentions, but not competitive or cooperative blocks, affected the use of prediction error.

We reasoned that when facing an individual who can change his/her intentions to compete or cooperate over time, the brain may rely on distinct experts to compute the best choice based on these

two possible intentions (i.e. cooperative or competitive), weighted by their relative reliabilities. We therefore built such an 'arbitrator' computation as a sigmoid function of the difference in reliability between the Cooperative and Competitive interactions (Δ), added to a bias (δ) that characterized each individual's tendency to attribute competitive (δ >0) or cooperative (δ <0) intentions to others. To assess intentions of the other, participants only have access to the outcomes of previous interactions, the choice (to stay or switch) of the artificial agent on previous trials, and the interaction between these two types of information.

We hypothesized that repeated social victories should favor the attribution of cooperative intentions because a series of victories suggests that both players are satisfied with the outcome. In such situations the other player (i.e. AA) has become more predictable, which is an important feature to build cooperation ⁴⁷. Moreover, the interaction between outcome and AA's choice (i.e. the tendency of the AA to "stay" after a participant wins or "switch" after a participant loses) should drive the arbitrator to favor the cooperative mode, because playing the same winning target for both players corresponds to the optimal Nash equilibrium of the cooperative game. To test this hypothesis, we regressed the signed difference in reliability on (1) the participant's last outcome, (2) AA's choice to "stay" or to "switch" and (3) the interaction between the participant's outcome and the AA's choice to stay or switch (Cooperativity signature) over up to three retrospective trials. We found that the past two interactions between participant's outcome and AA's action (Cooperativity signature), the last outcome and switches AA t-2 t-3 explained by the at trial and the difference in reliability (Cooperativity signature t_{-1} : estimate =0.59, p<0.0005; Cooperativity signature $_{t-2}$: estimate =0.06, p=0.037; *Victory*: estimate = 1.98, p<0.0005; switch $_{t-2}$: estimate =-0.18, p<0.0005; switch $_{t-3}$: estimate =-0.07, p<0.0005), χ^2 test, Fig. 4a).

Together, these analyses show that participants' behavior, when alternating between unsignaled cooperative and competitive blocks, is best explained by the Mixed-Intention Influence model. According to these findings, people use mentalization to update their beliefs about future chosen targets, and dynamically arbitrate between the predicted intentions of the other agent to compete or cooperate (**Fig. 3a**).

Model-based fMRI analyses

214

215

216

217

218

219

220

221

222

223

224

225

226

227

228

229

230

231

232

233

234

235

236

237

238

239

240

241

242

243244

245

246

247

248

First, we constructed a GLM (GLM1) to identify brain regions tracking the arbitration process (i.e. Δ : signed reliability difference, reliability for cooperation minus that of competition) between the two experts (one for cooperation, the other for competition). We added the reliability difference Δ as parametric regressor at the decision stage, and the expected reward for staying on the same target, as non-orthogonalized parametric regressors to allow them to compete for the variance. We added the

reward prediction error as a parametric regressor at the outcome time and we controlled for the other's intention effect by adding Δ as a non-orthogonalized regressor. The bilateral ventral striatum (x,y,z=9,12,0 and x,y,z=-12,9,-6,), vmPFC (x,y,z=6,45,-8), postcentral gyrus (x,y,z=-20,-44,48), and middle cingulate cortex (MCC; x,y,z=11,-15,57, p<0.05 whole-brain family-wise error (FWE), **Fig. 4b** and **4c**) tracked the difference in reliability between experts (Δ) at the decision time. Bilateral dorsal striatum (DS; x,y,z=17,6,-12 and -14,3,-11), bilateral orbitofrontal cortex (OFC; x,y,z=44,36,-14 and -44 52 8), posterior cingulate cortex (PCC; x,y,z=2,-34,38), and bilateral angular gyrus (x,y,z=45,-30,46 and -54,-62,39) (p<0.05 FWE, **Fig. 5a**) encoded the reward prediction error at the outcome time.

To investigate brain areas encoding the reward prediction error that were more engaged when the controller classified a trial as competitive vs cooperative, we tested another GLM (GLM2). Trial onsets were separated according to whether the value of the signed reliability difference Δ added to the bias was positive or negative. If this value was ≥ 0 , the trial was classified as Cooperative, and Competitive otherwise. The computed expected reward for staying on the same target was used as a parametric regressor at the time of choice. We found that the right dIPFC (x,y,z=35,11,36), the IPS region (x,y,z=50,-50,32) and the right temporoparietal junction (rTPJ; x,y,z = 51,-50,33, p<0.05 FWE) were more engaged in encoding reward prediction error in trials classified as Competitive versus Cooperative (p<0.05, FWE **Fig. 5b and 5c**). This effect could not be explained by less variance in the PE regressor in trials classified as Competitive trials compared to those classified as Cooperative, because we observed no difference in regressor variance on these two types of trials (p=0.57, Levene's test). No region was more engaged in trials classified as Cooperative compared to those classified as Competitive.

To further investigate the relationship between the behavior to stay after a trial classified as Competitive *versus* classified as Cooperative and the BOLD signal, we conducted a logistic regression. Explanatory variables were the average of the weighted time series in the dIPFC and rTPJ/IPS region observed in GLM2, the valence of the controller (Δ) and their interactions. This signal was extracted at the time of the outcome and convolved with the hemodynamic function. Because there was an average of 6.6 scans per trial, we took as a predictor variable the mean of this weighted signal through the 7 scans following the outcome presentation. We found an interaction between the weighted time series and the valence of the arbitration (*valence of the arbitration*_t * *weighted time series*_{t-1}: *estimate* = -14.4, p = 0.0312, χ^2 test). Post hoc tests further revealed that this effect was driven by trials classified as Competitive (*weighted time series*_{t-1} of trial classified as competitive_{t-1}: *estimate* = -37.3, p = 0.040, χ^2 test). This result indicates that activation of rdIPFC and rTPJ/IPS increases the probability of switching following a trial classified as Competitive.

 $logit(P(stay)) = \beta_0 + \beta_1 * sign(\Delta) + \beta_2 * Time Series + \beta_3 * sign(\Delta) * Time Series$

Connectivity analysis

Finally, we performed a generalized psycho-physiological interaction (gPPI) seed to voxels connectivity analysis to understand the interactions between brain regions tracking the arbitration process (i.e. Δ: reliability difference) for the cooperative and competitive experts and those more engaged with the PE when the controller attributes more competitive than cooperative intentions to the other (see Online Methods). We used the ventral striatum and vmPFC, which encoded the controller, as seed regions (ROI extracted from the GLM1 striatal and vmPFC activity) for trials classified as competitive compared to those classified as cooperative (i.e. trials for Δ<0 or Δ>0) at the decision time. We found stronger functional connectivity between regions encoding the difference in reliability and the right dIPFC (x,y,z=38,34,34), the left IPS region (x,y,z=-48;-44;58) and the left TPJ (x,y,z=-42,-40,50, p<0.05 FWE; Fig. 6a) at the decision time for trials classified as Competitive compared to those classified as Cooperative. This result indicates that the dIPFC, IPS and left TPJ receive an input signal at the time of choice according to the difference in reliability with respect to the Competitive *versus* Cooperative believed intention of others. This brain network largely overlaps with the brain network observed with the PE differentiating between trials classified as Competitive *versus* Cooperative at the outcome (Fig. 5b and Extended Fig. 4).

Discussion

To make a strategic decision when facing an individual with unknown and fluctuating intentions. it is necessary to make inferences as to whether we are in a competitive or cooperative situation. In the context of minimal information, for example when only the choices of the other, but not their outcomes, are available, such inferences are much more difficult than when one is in a specific known setting (e.g., in a competitive game) 19. Here, we provide evidence that the brain engages in dynamic tracking of another individual's cooperative/competitive intentions, despite having no explicit information regarding whether the situation is cooperative or competitive. We found that strategies of participants were mostly affected by the outcomes of previous interactions and by a "signature" of the other's cooperativity, i.e. the tendency of the other (here the Artificial Agent or AA) to stay on the same target after the participant's winning. Comparison between computational models demonstrated that such behavior is best explained by a model in which choice is driven by a controller tracking the reliability difference between cooperative and competitive intentions. The fMRI results show that the neural computations of this controller are implemented in the ventral striatum and in the vmPFC. Thus, both behavior and brain imaging results can be accounted for by a model that includes a controller that allocates resources according to different experts' predictions. At the time of outcome, a common brain network, including the rostral anterior cingulate cortex (rACC), ventral striatum and lateral OFC encoded prediction error in trials classified as Competitive or as Cooperative. However, prediction error signals in some brain areas also depended on the classification of the current trial as Cooperative or Competitive as classified by the controller. That is, a distinct brain network, composed of the bilateral dIPFC, bilateral IPS regions and the rTPJ was more engaged for trials classified as Competitive compared to those classified as Cooperative. This latter brain network reflects a differential use of the outcome of the social interaction as a function of whether it is classified as Competitive or Cooperative (Fig. 2d).

Mentalizing processes are essential to correctly infer the strategy of others. This is true in the cooperative context, in which participants performed above chance, reflecting their ability to effectively infer the other's (i.e. AA's) behavior. In the competitive context, participants performed below chance level, showing that the AA was able to predict their behavior and to exploit their previous choices/outcomes. The Mixed-Intention Influence model had the best ability to predict data and to generate very similar behavior to the participants. Each expert model is an expanded RL model, with a term accounting for one's previous choice influencing the choice of the other. Although only the influence term differed between the Competitive and Cooperative models, the Mixed-Intention Influence model tracked intentions based on this second order mentalizing term by weighting the contribution of a cooperative and of a competitive expert. One key aspect of this Mixed-Intention Influence model is that it captures higher order structures (fluctuations between cooperation and competition) during social interactions. In contrast, one important limitation of the classical RL model is that it does not exploit higher-order structures such as interdependencies between different stimuli, actions, and subsequent

rewards. Previous studies demonstrated that models incorporating such structures can account for individual decision making in different situations ^{48–51}. Here, we demonstrate that the representation of abstract states, such as whether the other is cooperating or competing, can be extended to social decisions and underlies the ability to build strategies. To confirm that the Mixed-Intention Influence model accounted more for neural activity in brain areas involved in social interactions, we formally compared the brain regions covarying more with the expected reward for staying on the same target, as computed by the winning model, compared to the expected reward for staying on the same target, computed by a simple RL model (**Extended Fig. 3**). One crucial difference between a simple RL model and the Mixed-Intention Influence model is that in the former, only the value of the chosen option is updated and the valuation of the option that was not chosen does not change. In the latter, both the values of the chosen and unchosen options are updated to incorporate the knowledge that the current state has a given reliability to be cooperative or competitive. The controller weights the valuation produced according to the competitive or cooperative hypothesis which is computed as a sigmoid of the difference in reliability between the two experts.

Activity in the ventral striatum and vmPFC increased as the cooperative prediction from the controller became more reliable than the competitive prediction, as a result of the outcomes of the previous interactions (reliability difference modulated by last outcome) and the other's "Cooperativity signature" over the last trials. Thus, these brain regions dynamically track the reliability difference between intentions classified as cooperative and competitive in a situation where the nature of the social interactions is implicit. Previous reports demonstrated a role of the ventral striatum when making cooperative choices alone, in response to a partner's cooperative choice in an explicit cooperation task ⁵² and also in the attribution of intentions in a competitive context ³⁰. Our findings show that strategic social behavior can be explained by a Controller Theory according to which cooperative/competitive social behavior results from the interaction of multiple systems, each proposing possible strategies for action ^{26,28,29}.

One strength of our computational approach was to assess and compare a large variety of competing models, (active inference, recursive learning models k-TOM and a mixture of experts using k-TOM, influence models for only cooperative strategies or competitive strategies, a mixture of experts using influence models, fictitious learner, Bayesian Sequence learner, Hierarchical Gaussian Filter, Reinforcement Learning and Heuristic models). Many have never previously been directly tested against each other. Our results agree with studies concluding thatsocial learning may be driven by non-specific reinforcement processes that include a mentalizing term ^{3,6,8,30,53}. We demonstrate that when a task is not explicitly signaled as cooperative or competitive, this evokes the arbitration between strategies determined by predictive reliability. Behavior is hence controlled by giving a higher weight to the strategy with the most reliable prediction ²⁹. At first glance, it may be surprising to observe that the mixture of expert influence models performs better than mathematically more sophisticated models,

such as POMDP models (HGF, active inference, k-ToMs) and models mimicking different levels of mentalizing (k-TOM). However, this is likely because in our setting the only information that can be integrated by participants is their own choices, rewards and the history of the choices made by the other (i.e. AA). The nature of the social interaction is never explicitly signaled (participants are not told whether the other is cooperative or competitive), and the rewards of the other are not observed. This uncertainty could therefore result in the failure of POMDP models to reproduce human behavior, particularly when sudden flips occur between the AA strategies. This contrasts with previous neuroimaging studies that investigated learning of social interactions in either competitive or cooperative situations alone (matching-pennies or rock-paper-scissors games against computerized opponents) ^{25,54}. Our findings also broadly agree with a cognitive hierarchy of strategic learning mechanisms, proposing that distinct levels of strategic thinking correspond to different levels of sophistication of learning mechanisms (in increasing order of complexity: reinforcement learning, fictitious play learning and influence learning) ⁵⁵. However, we propose a more general model based on a mixture of influence learning experts that function in parallel and are then compared with respect to their relative reliability.

Competitive social interactions often emerge in situations where an agent's outcome depends on the choices of others, which requires the ability to infer the intentions of others 6. In the context of our mixed intentions task, when participants attributed competitive, as opposed to cooperative intentions to others, the dIPFC and rTPJ/IPS specifically encoded a relative PE. Although this network has previously been reported when inferring the intentions of others 8,39,56, the strength of our computational account of theory of mind processes is to specify that this brain network computes a PE difference between trials that the controller classified as competitive versus cooperative. This PE difference reflects a differentiation in the implementation and use of the outcome of the social interaction as a function of the classified interaction (Fig. 3c). Note that PE was not more volatile in trials when the competitive expert is more reliable than the cooperative expert. This rules out the possibility that the observed PE difference reflects higher PE volatility in competitive contexts. When comparing intentions classified as cooperative compared to competitive, participants tended to be more predictable, staying more on the same target after experiencing an unexpected social defeat (i.e. after higher negative PE) (Fig. 3c). This behavior likely reflects a signal sent to the other to indicate one's willingness to stay on the same target, despite bearing the cost of staying on this target ^{6,8,57}. This is a key feature of successful coordination ⁴⁷ in which agents who want to trigger reciprocity ⁵² are willing to incur a cost to promote cooperation from the other.

Finally, we found higher functional connectivity between seed regions that encode the reliability difference of the controller (vmPFC and striatum) and brain regions more engaged in PE for trials classified as Competitive *versus* Cooperative (dlPFC, TPJ) (**Fig. 6**). This indicates that brain regions engaged in the input of the arbitration process at the time of choice are more strongly coupled (resp. decoupled) with brain regions encoding PE for intentions classified as Competitive (vs Cooperative).

This reflects a differential use of the outcome of the social interaction as a function of whether it is classified as Competitive or Cooperative. Thus, according to the attributed intention of other by the controller, PE signals differed and the strength of functional coupling increased between regions encoding the reliability difference of the controller and the dIPFC-TPJ network. When one expert is more reliable than the other, the Mixed-Intention Influence model predicts that the reward PE is driven by the valuation of the more reliable expert. Since the only difference between experts is the sign of the second-order mentalizing term, this suggests that the implication of the dIPFC-TPJ network at the outcome is engaged when there is a need to mentalize intentions of other agents with opposing goals (i.e. intentions classified as Competitive). Moreover, engagement of the dIPFC-TPJ network increases the probability of switching following a trial classified as competitive by the controller, allowing behavioral adaptation by virtue of the reliability difference signal.

Together, our work provides evidence that the mixture of experts model explains behavior in socially volatile situations differing only by the reward function of other agents. These two experts only differ by their priors on how their reward function takes into account another agent's reward (i.e. the second order mentalizing term), and were sufficient to discriminate the others' intentions. These findings provide a mechanistic framework explaining the neurocomputations underlying learning in strategic social interactions. We extend to theory of mind processes (i.e inferring cooperative vs competitive intentions) a computational account similar to mixture of experts proposed to arbitrate between strategies in other domains, such as exploitation vs exploration ^{58,59}, "model-based" vs "model-free" systems ^{26,28,60} and learning by imitation vs emulation ²⁹. Finally, our Mixed-Intention Influence model may be useful in the field of computational neuropsychiatry to identify the specific computational components that are modified in theory of mind alterations, a key feature of autism spectrum disorder ⁶¹.

Author contributions

J-C.D., R.P, R. P.N.R, and D.L. developed the general concept, experiment and models. R.P. programmed the task and ran the experiment under the supervision of J.-C.D. R.P. developed the models and implemented the algorithms under the supervision of J.-C.D., and analyzed the data in collaboration with J.-C.D. R.P. and J.-C.D. wrote the manuscript in collaboration with K.K., D.L and R.P.N.R.

Acknowlegements

This research has benefited from the financial support of IDEXLYON from Université de Lyon (project INDEPTH) within the Programme Investissements d'Avenir (ANR-16-IDEX-0005) and of the LABEX CORTEX (ANR-11-LABX-0042) of Université de Lyon, within the program Investissements d'Avenir (ANR-11-IDEX-007) operated by the French National Research Agency. This work was also supported by grants from the Agence Nationale pour la Recherche and NSF in the CRCNS program to JCD (ANR n°16-NEUC-0003-01), and by CRCNS NIMH grant no. 5R01MH112166-03, NSF grant no. EEC-1028725, and a Templeton World Charity Foundation grant to RPNR.. We thank the CERMEP Staff for help during scanning and Pr Ed Derrington for proof reading the draft of the manuscript.

Competing interests

The authors declare that they have no competing interests.

Resources availability

Lead contact

- Further information and requests for resources and inquiries should be directed to and will be fulfilled by the lead contact, Jean-Claude DREHER (dreher@isc.cnrs.fr).
- This study did not generate new unique reagents.

Materials availability

This study did not generate new unique reagents.

Data and code availability

461 Code supporting main results are available at GitHub 462 (https://github.com/remiphilipp/Mixture intention.git).

Method

Participants

32 participants (aged 20-40, M = 27, SD = 5.1 - 17 women) were recruited via a daily local newspaper and the University of Lyon 1 mailing list. All participants were screened to exclude those with medical conditions including psychological or physical illnesses or a history of head injury to prevent having confounding variables. They all provided informed consent and were paid a fixed amount. However, they were financially motivated in being told that they would be paid as a function of their decisions.

Mixed intentions task

Participants performed a novel task comprising 163 trials in an MRI scanner. They were led to believe that they were interacting with another person via a computer interface, while in fact they were playing against an artificial agent (AA) managed by a computer program. Such simulated social interactions allowed us to investigate the dynamics and neural mechanisms arbitrating between multiple learning algorithms. Participants were faced with a screen containing four cards, two face down (the other player's cards) and two face up (their own cards). Participants were informed that to win, they had to choose the card of the same color as the one the other person was going to choose. Experimenters were careful not to specify whether the other was an adversary or a partner. Participants were told that they and the other player had to make their choices in four seconds (Fig. 1a). If the Artificial Agent (AA) played before the participant, one of the two face down cards was removed from the playing field. If the participant chose first, only the selected card remained on the playing field. Then, when both had chosen, the chosen cards were revealed and the participant received a reward if the card colors matched, otherwise they received nothing. Participants were led to believe that their final payoff would be increased by 10 ct (euro) for each winning interaction. No information about the other's payoff was given to the participants, they only knew that after an interaction, the other 'participant' would see the same screen but with their outcomes which could be different from the participant.

Importantly, <u>unbeknownst</u> to the participants, the artificial agent alternated between Competitive and Cooperative trial blocks. During this mixed intentions task, the AA's strategy was determined by alternating 13 trials of a hide and seek (HS) task (Competitive blocks), and 10 trials of a coordination game (Cooperative blocks). The artificial agent algorithm was designed to predict the color that would be chosen by the participant on the basis of a probabilistic analysis of the two previous choices and outcomes (**see SI** for the algorithm). Here we defined a competitive choice, made by the AA, as choosing the card of the color the participant was expected not to play and a cooperative choice as choosing the card with the same color. Thus, the artificial agent exploited the bias of the participants in a stochastic way, i.e. the more predictable the participant was, the more the algorithm made correct competitive or cooperative choices (see SI). Participants were not informed of the switches between

the two blocks (Cooperative vs Competitive), however their goal was always to choose the same color as that chosen by the other player (i.e. the AA).

The HS task is competitive, and the computer uses the record of the participant's choice and reward history to minimize the participant's payoff. Therefore, in this case the subject's optimal strategy during the HS task is to choose the two targets equally often and randomly across trials. During the coordination game, the AA tried to maximize the subject's payoff and in this case the subjects should try to choose one of the two targets consistently so that the computer can choose the same target as them. Since the participant is not informed of either the goals of the AA or the switches between blocks, they must adjust their strategy based on recent experience and infer cooperation/competition on the basis of their observations.

This task was to designed to identify key components of the estimation of intentions regarding whether others are cooperating or competing. We took advantage of the fact that an individual's estimates as to whether they are engaged in a cooperative or competitive interaction can be assessed even when the individual is interacting with a computer program rather than another person. Transitions between the competitive and cooperative blocks were unsignaled, therefore subjects had to discover by trial and error the most successful strategy over consecutive blocks. This alternation between the two interaction modes functioned well because the participant's winning rate was significantly higher in cooperative (mean 60% std 1%) than in competitive (mean 44% std 1%) trials (paired t-test p<10⁻⁴).

Artificial agent

The AA calculated the probability p for the participant to select a particular target color based on the history of the two previous choices and their outcomes. Then to make the artificial agent behave more like a real person, this prediction was exploited in a probabilistic fashion (**see SI**). In the cooperative mode the AA chose the color card it predicted with probability p. In the competitive mode this color was chosen with probability 1-p.

Behavioral analysis

For the logistic regressions, we reported significant marginal effect of a given variable under the name "estimate" (for example: $Cooperativity signature_{t-1}$: estimate).

Logistic regression : $\ln\left(\frac{P}{1-P}\right) = x_0 + x_1X_1 + x_2X_2 + \cdots$

 X_i represents independent variables and x_i represents the associated weights in the logistic regression. P represent the probability of a given event. The marginal effect of the variable X_1 is defined as:

 $\widehat{y_1} = mean(logit^{-1}(x_1))$

The mean is computed across all observed data. Thus, the marginal effect called "estimate" can easily be interpreted as the discreet change of the dependent variable given a unitary change of an independent variable.

For the linear regressions, reported "estimate" represents x_i i.e. the regression coefficient. Indeed, in a linear regression, marginal effect of a variable is equal to the estimated coefficient.

Models

To test for a dynamic tracking of implicit intention we compared 14 models, 9 involved theory of mind (*Inf*,*k*-*ToM*), the others were to control for other possible strategies. The influence models (*Inf*) rely on aylor expanded reinforcement learning ⁶² to take into account the influence of one's own strategy on the strategy of the other. *k*-*ToM* models also take into account the influence of one's own strategy on the other but in a Bayesian fashion ^{13,35}. These two models were adapted in their cooperative and competitive versions. Moreover, we constructed an adaptation of these two models (*Inf*,*k*-*ToM*) in which an arbitrator weights the cooperative and competitive versions according to their reliability before making the decision. Finally, because k-ToM is a recursive model ("I think that you think that…), we included k-ToM of depth one and two for each version.

To control for strategies that did not include theory of mind we added 5 other models including two Bayesian inference types (*HGF* and *BSL*). The Hierarchical Gaussian Filter (*HGF*) ^{43,63} basically tracks the external volatility of the artificial agent choices in a Bayesian hierarchical way. The Bayesian Sequences Learner (*BSL*) strategy relies on Bayesian inference given past sequences of choices. In a model free analysis, we found that participants tended to use the past 2 choices to make their next choice, so we used sequences of depths 2 and 3. Finally, we added two non-Mentalizing non Bayesian models, a reinforcement learning model (RL) and a model based on the heuristic Win/stay – Lose/Switch that we observed in the model free analysis.

The Bayesian Model Selection (BMS) was performed using the VBA toolbox (Variational Bayesian Analysis) in a random effect analysis relying on the free energy as the lower bound of model evidence. We use protected Exceedance Probability measurements (pEP) ⁴⁵ to select the model which is used most frequently in our population.

Model	Mentalizing	Bayesian	Mixed intentions	
Influence	+ (coop and comp)	-	-	
Fictitious	+	-	-	
Influence mixed intentions	+	-	+	
k-ToM	+ (coop and comp)	+ (depth 1 and 2)	-	
k-ToM mixed intentions	+	+	+	
Active Inferences	-	+	-	
HGF	-	+	-	
BSL	-	+ (depth 2 and 3)	-	
RL	-	-	-	
Wst/Lsw	-	-	-	

Table 1. Classification of models according to 3 categories. The first depends on the ability of the model to mentalize, the second depends on whether the model is a Bayesian model, and the third concerns models that could be used with a mixture of experts.

fMRI data acquisition

MRI acquisitions were performed on a 3 Tesla scanner using EPI BOLD sequences and T1 sequences at high resolution. Scans were performed in a Siemens Magnetom Prisma scanner HealthCare at CERMEP Bron (single-shot EPI, TR / TE = 1600/30, flip angle 75°, multiband acquisition (accelerator factor of 2), in an ascending interleaved manner with slices interlaced 2.40 mm thickness,

FOV = 210 mm. We also use the iPAT mode with an accelerator factor of 2 and the GRAPPA method reconstruction. The number of volumes acquired varied given the time the participant took to make their decisions. The first acquisition was made after stabilization of the signal (3 TR). Whole-brain high-resolution T1-weighted structural scans (0.8 x 0.8 x 0.8 mm) were acquired for each subject, co-registered with their mean EPI images and averaged across subjects to permit anatomical localization of functional activations at the group level. Field map scans were acquired to obtain magnetization values that were used to correct for field inhomogeneity.

fMRI data analysis

Image analysis was performed using SPM12 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, UK, <u>fil.ion.ucl.ac.uk/spm/software/spm12/</u>). Time-series images were registered in a 3D space to minimize any effect that could result from participant head-motion. Once DICOMs were imported, functional scans were realigned to the first volume, corrected for slice timing and unwarped to correct for geometric distortions. Inhomogeneous distortions-related correction maps were created using the phase of non-EPI gradient echo images measured at two echo times (5.20 ms for the first echo and 7.66 ms for the second). Finally, in order to perform group and individual comparisons, they were co-registered with structural maps and spatially normalized into the standard Montreal Neurological Institute (MNI) atlas space using the DARTEL method. Then we ran ARTrepair to deweight scans that could include movement artefacts ⁶⁴.

We ran general linear models (GLMs) analyses to identify which brain regions encoded: (a) one's belief that one is interacting in a cooperative or in a competitive situation (Δ); (b) the reward prediction error (PE) after interactions classified as cooperative or competitive; (c) the PE difference between the trials classified as cooperative vs competitive. In every GLM, an event was defined as a stick function. The participant's button press and the AA's selection of target were defined as onset of no interest in all GLMs. For all GLMs, missing trials were modeled with four events (cue, participant's button press, AA's choice and outcome) as separate onsets without additional parametric regressors. Head movement parameters were added as parametric regressors of no interest to account for motion-related noise. Because the behavioral analysis showed that the bias towards competitive interaction affects the strategy of participants, we added the competitive bias (δ) as a covariate at the second level analysis in all GLMs.

Specifically, in GLM1, there were 4 onsets, including the time of the cue presentation (cards on screen), participant's button press, AA's choice and the feedback time. Parametric regressors were the difference in reliability Δ , the expected reward for staying at the time of the cue onset and the reward prediction error (PE) at the feedback time, as well as Δ , to control for the effect of the believed intention

of the other on the PE brain encoding. For each GLM, we turned off the serial orthogonalization function of regressors to allow it to compete for the variance.

In a second GLM (GLM2), we separated trials given the sign of Δ - δ (positive or negative) to identify brain regions specifically engaged in cooperative or competitive mental states (δ is a free parameter capturing the participant's bias toward competitive intent). Δ refers to the difference in reliability of cooperative and competitive prediction and δ is the competitive bias. For this GLM, there were 6 onsets, including the cue for trials classified as cooperative or competitive, participant's button press, AA's choice and the feedback time for trials classified as cooperative or competitive. Trials were classified as either cooperative or competitive and parametric modulators were: the difference in reliability Δ and the expected reward for staying on the same target at the time of the cue and the PE and Δ at the time of feedback. Three participants who always attributed the same intention to the AA were not included in GLM2.

To test the additional hypothesis that brain activation observed for believed other's intentions (in **Fig. 4b**) is also present in competitive vs cooperative blocks, we conducted two more GLMs. The first, GLM3 is similar to GLM2, i.e., we separated trials into two categories (cooperative and competitive), but the differentiation was made using the real mode of interaction of the AA rather than the classification made by the controller. Other onsets and parametric regressors were left unchanged.

Finally, a last GLM was applied to check that the results observed in GLM2 were not simply due to the effect of volatility of the rewarded target. This GLM (GLM4) is similar to GLM2, i.e. trials were classified according to the sign of Δ - δ . The only difference was that we added the actual probability that the AA would choose the same target as the previous trial as a parametric regressor at both the time of the cue and at the outcome.

We computed one sample t-tests with contrasts for main effect of Δ in GLM1 and effect of PE at the outcome time. Then we computed the contrast between competitive and cooperative PE regressors in GLM2, GLM3 and GLM4. Finally, we computed a paired t-test between this contrast, derived from GLM2 and GLM3, to formally show that activation coming from the difference between classified trials was significantly higher than those coming from the difference between the actual modes of interaction as determined by the trial block.

Reported brain areas show a significant activity at the threshold of p<0.05, whole brain family-wise error (FWE), corrected for multiple comparisons at the cluster level (threshold at P<0.001 uncorrected).

Psychophysiological interaction (PPI) analysis

We defined the attribution of cooperative or competitive intentions at the time of decision making as the psychological factor. Thus, we were able to investigate the difference in functional connectivity when making a decision under cooperative or competitive intent. For this PPI analysis, we focused on decision time and on functional connectivity between regions encoding the others' intentions and all other voxels. Thus, for the physiological factor we took the BOLD signal of the striatal region elicited in GLM1 as encoding the intention of others. Otherwise, we used same regressor parameters and onsets as GLM2.

Reported brain areas show a significant activity at the threshold of p<0.05, whole brain family-wise error (FWE) corrected for multiple comparisons at the cluster level (threshold at P<0.001 uncorrected).

Figures

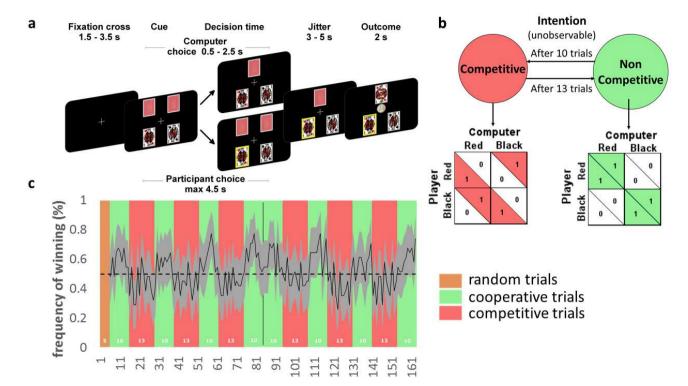


Figure 1. fMRI experiment. **a**. After a fixation cross, four cards were presented on the screen. The two cards shown on top of the screen represent the cards presented to the opponent/partner (i.e. Artificial agent), and not seen by the participant while the two kings (one black and one red) are the cards presented to the participant (shown in the bottom of the screen). The participants had to choose between these two cards. At the time of decision, the upper screen represents the display if the AA makes it choice first, while the lower screen shows how one card is highlighted with yellow border if the participant makes his choice first. Then a screen presents the participant's and Artificial Agent's choices together. Finally, at the time of outcome the participant wins if both he/she chooses the same card as the AA (here red king). **b**. Payoff matrix of the two types of block. **c**. Frequency of winning (black line) during competitive (red background) and cooperative (green background) blocks. The grey area represents the 95% confidence interval. The orange background represents 5 initial trials in which the AA played randomly for initialization purpose.

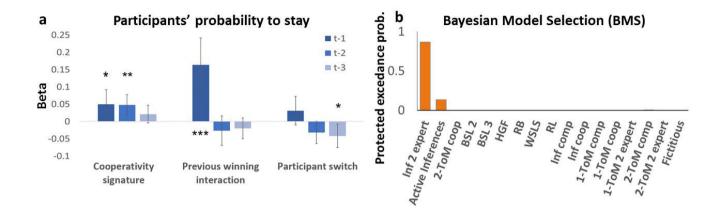


Figure 2. a. Model-free analysis. Random-effect logistic regression of the decision to stay after selecting a specific target with respect to the action of the artificial agent "Cooperativity signature" (i.e. participant wins then AA stays or participant loses then AA switches), the previous winning interaction (i.e. success or failure of past trials) and the choice to switch or stay, over the previous three trials. Error bars are the 95% confidence interval. **b.** Model comparisons based on Bayesian model selection. The protected exceedance probabilities indicate that the Mixed-Intention Influence model (Inf 2 expert) explains decisions in the mixed intention task better than others: Active inference; k-ToM; Bayesian Sequence Learner (BSL); Hierarchical Gaussian Filter (HGF); Reinforcement Learning (RL); Heuristic models: Random Bias (RB); Win/Stay-Lose/Switch (WSLS).

679

680

681

682

683

684

685

686

687

688

689

690

691

692

693 694

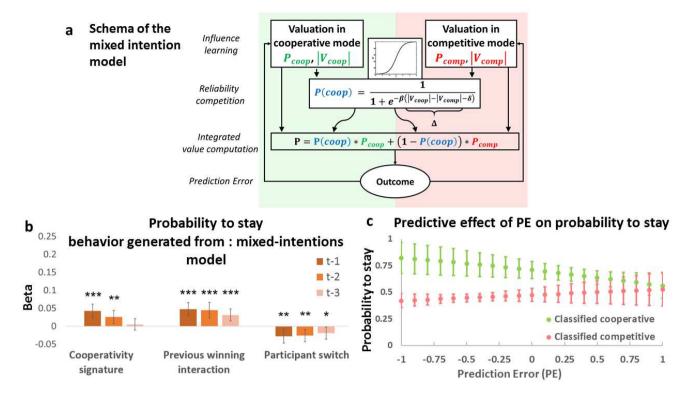


Figure 3. a. Scheme of the Mixed-Intention Influence model. Two influence models (one cooperative and the other competitive) compute a value for choosing one specific target (the black one). A controller uses the difference between the absolute value of the value of each expert (called reliability) to compute a probability that the other is cooperating. Then, the model weights the value of each expert according to the probability of being in cooperative and in competitive modes to produce a final decision value. Then it compares its predictions to the actual reward and compute again a new value for each expert. b. Model-free generative analysis. We generated one hundred sets of data using a free parameter from a normal distribution with mean and standard deviation calculated from the models fitted to the population, against the same artificial agent that participants played. We regressed the behavioral decision to stay after selection of a specific target on the previous trial depending on the interaction of the previous outcome and the action of the artificial agent ("Cooperativity signature"), the success or failure of up to three previous trials, and the action to switch or stay of the participant. Error bars are the 95% confidence interval (random-effect logistic regression). c. Marginal effect of the prediction error on the probability to stay on the same target in trials classified as Cooperative (green) and trials classified as Competitive (red). Error bars are the 95% confidence interval. *p < 0.05, **p < 0.01, ***p < 0.001 (random-effect logistic regression).

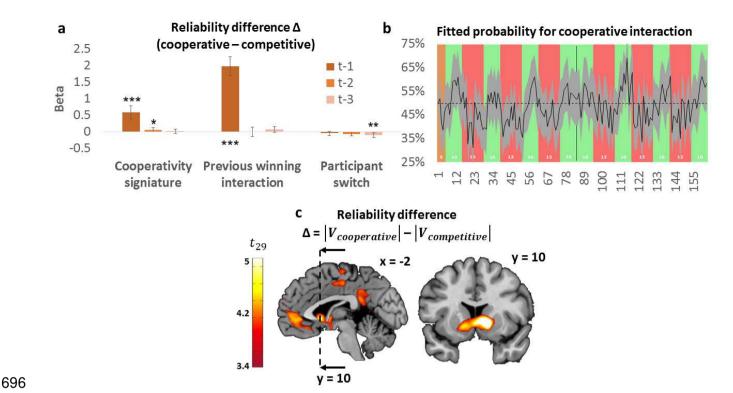


Figure 4. a. Difference in reliability is influenced by the Cooperativity signature of the Artificial Agent (AA), specifically the interaction of the previous subject's outcome followed by the action of the artificial agent (Participant wins then AA stays and Participant loses then AA switches), the latest outcome and the computer's switch at trial t-2 and t-3. Error bars are the 95% confidence interval. **b**. Mean probability of the participant attempting to cooperate across all participants (black line) for the 163 trials. The initial orange area is the 5 random initializing trials, green areas are the Cooperative blocks and red areas the Competitive blocks. The grey area is the 95% confidence interval. **c**. BOLD signal in ventral striatum, mPFC and posterior cingulate cortex (PCC) (p < 0.05 whole-brain family-wise error) are correlated with the difference in reliability, Δ, of estimated competitive and cooperative intentions.

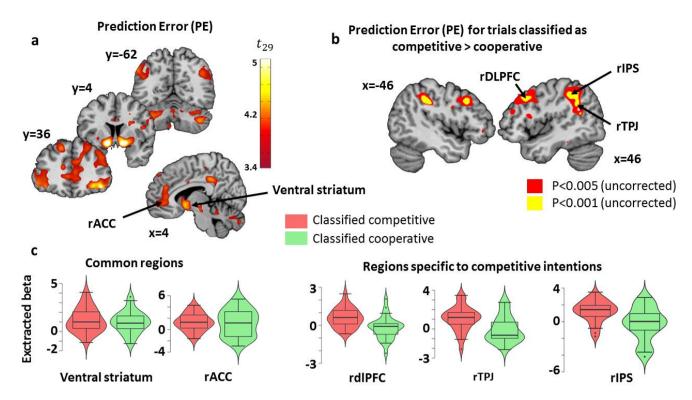


Figure 5. Correlations between BOLD activity and prediction error. **a.** Brain regions in which BOLD signal correlates with prediction errors for trials classified by the controller to be either competitive or cooperative. **b.** Brain regions in which BOLD activity correlates more with PE on trials estimated to be competitive compared to trials estimated to be cooperative. This network comprised dIPFC (x,y,z=30,9,42), IPS (x,y,z=42,-47,42) and the rTPJ (x,y,z=51,-50,33,p<0.05) whole-brain family-wise error). **c.** Beta value extracted for trials estimated to be either competitive or cooperative. Left: regions in the ventral striatum (left x,y,z=-14,3,-11+right x,y,z=17,6,-12) and rACC (x,y,z=6,42,-3) with increased activation in trials estimated to be either competitive or cooperative. Right: specific brain regions activated only when trials were classified as Competitive: dIPFC (x,y,z=30,9,42), IPS (x,y,z=42,-47,42) and rTPJ (x,y,z=51,-50,33) from 8 mm spheres centered on peak activation.

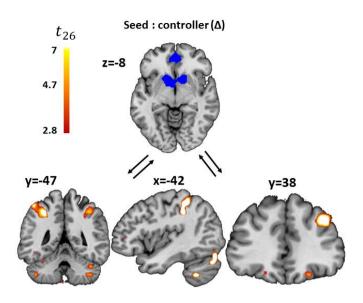


Figure 6. Neural mechanisms of arbitration between the attributions of competitive and cooperative intentions to the AA. Connectivity analysis: the BOLD signal was extracted from seeds regions (mPFC and ventral striatum using GLM1) computing the reliability difference between cooperative and competitive intentions of others (in Blue). The psychophysiological interaction effect shows higher functional coupling (voxels in red) with the left TPJ (x,y,z=-42,-40,50), left IPS (x,y,z=-32,-48,50) and right dIPFC (x,y,z=38,34,34,p<0.05 FWE threshold at p<0.001) in trials classified as competitive as compared to those classified as cooperative.

Extended data

Extended table

731

732

733

734

729

730

Extended results table of GLM1, related to Figure 4c.

Table 1. Brain region that covaries with difference in reliability of interaction mode

	MNI pe				
	Х	у	Z	k	Z score
Difference in reliability (Δ=Rcoop -Rcomp)					
Ventral Striatum	14	9	-2	3375	4,99
Left hippocampus	-35	-53	3	660	4,3
mPFC	6	45	-8	1580	4,24
Right hippocampus	32	-36	12	3836	4,11
Middle cingulate cortex	11	-15	57	1732	3,95
Left Angular	-32	-53	27	857	3,86
Left postcentral gyrus	-20	-44	48	661	3,85
Rcomp – Rcoop					
No brain region					

^{**} cluster reported at p<0.05 FWE whole brain cluster corrected (initial cluster-forming threshold of p<0.001 uncorrected)

738

Table 2. Brain region encoding both competitive and cooperative prediction error.

	MNI pe	ak cluster coo	rdinates		
	Х	у	Z	k	Z score
Positively					
Right Dorsal Striatum	17	6	-12	21895	8,79
Left Dorsal Striatum	-14	3	-11	3488	8,78
Left Cerebellum	-44	-74	-45	6381	5,49
Right Cerebellum	29	-71	-29	5299	5,33
PCC	2	-35	38	1285	5,3
Right Angular/TPJ	45	-30	47	3581	4,71
Left Angular/TPJ	-54	-62	39	2044	4,34
Left Angular/TPJ			39		
Negatively					
No brain region					

No brain region

^{**} cluster reported at p<0.05 FWE whole brain cluster corrected (initial cluster-forming threshold of p<0.001 uncorrected)

739

Table 3. Brain region that responded differently for the reward prediction error of a trial estimated to be competitive rather than cooperative

MNI peak cluster coordinates						
	Х	У	Z	k	Z score	
Competitive > Cooperative						
Right dIPFC	35	11	36	1732	4,41	
Right Angular/TPJ	50	50	32	1758	4,32	
Medial superior frontal gyrus	-2	30	47	505	3,82	

Cooperative > Competitive

No brain region

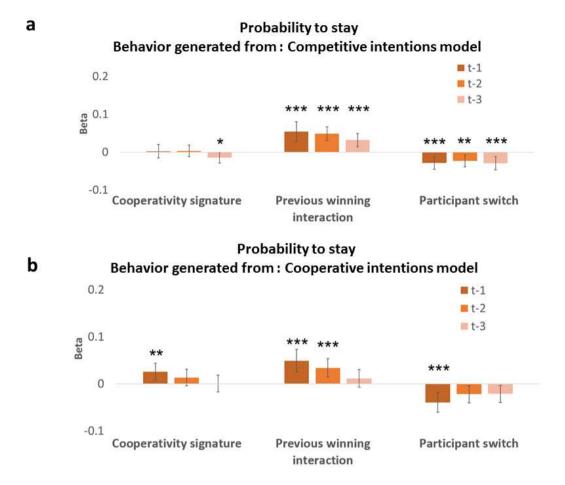
^{**} cluster reported at p<0.05 FWE whole brain cluster corrected (initial cluster-forming threshold of p<0.001 uncorrected)

Extended results table of connectivity analysis, related to **Figure 6.**

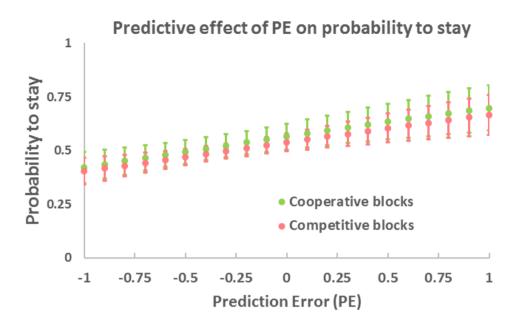
Table 4. Effect of the intention attribution at the decision time on the striatum/mPFC and dIPFC/TPJ connectivity strength.

gPPI Analyse	Seed	Peak regions	k	p-val unc.	p-val FWE	Z score
Competitive >	mPFC + striatum	-48 -44 58	363	<0.0005	<0.0005	4.52
	mPFC + striatum	-2 -82 -36	153	<0.0005	0.037	4.34
	mPFC + striatum	38 34 34	150	<0.0005	0.040	4.33
	mPFC + striatum	-38 -78 -26	181	<0.0005	0.017	4.27
Cooperative > Competitive	mPFC + striatum	4 -46 16	744	<0.0005	<0.0005	4.48

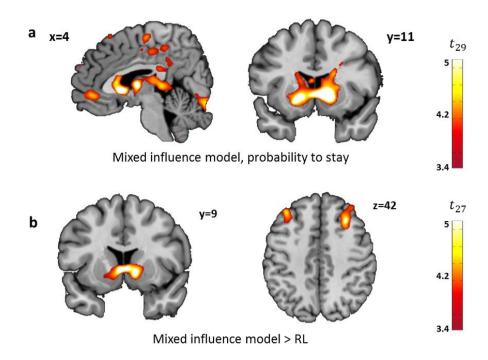
Extended figures



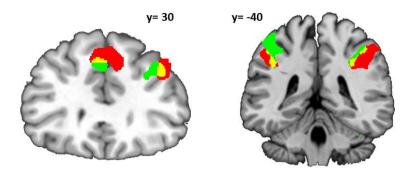
Extended figure 1. Model-based generative analysis. We generated one hundred sets of data using free parameters from a normal distribution with mean and standard deviation calculated from the "Influence models" in competitive (a) and cooperative (b) mode, fitted to the population. We generated a data set against the same artificial agent that participants played. We regressed the interaction of the previous outcome and action of the artificial agent (I win – AA stay / I lose – AA switch), the behavioral decision to stay after selecting a specific target at the previous trial based on the success or failure of the previous trial (Win) and the action to switch or stay of the artificial agent (Switch) in previous trials up to three trials back. Error bars are the 95% confidence interval. *p < 0.05, **p < 0.01, ***p < 0.001 (random-effect logistic regression). Related to Computational models tracking intentions of the other agent in the Result part.



Extended figure 2. Marginal effect of the prediction error on the probability to stay on the same target in Cooperative blocks (green) and in Competitive blocks (red). Error bars are the 95% confidence interval. *p < 0.05, **p < 0.01, ***p < 0.001 (random-effect logistic regression). Related to Computational models tracking intentions of the other agent in the Result part.



Extended igure 3.a. Neural correlates of the expected reward for staying on the same target as the previous trial, computed by the Mixed-Intention Influence model. (Significant ventral striatum correlation x,y,z=14,11,-2, p<0.05 FWE corrected threshold at p<0.001) **b.** Ventral Striatum (x,y,z=6,12,0), bilateral dIPFC (x,y,z=-36, 33, 44 and x,y,z=30,24,42) and MTG (x,y,z=65,-56,-8, p<0.05 FWE corrected threshold at p<0.001) are best explained by the expected reward for staying of the Mixed-Intention Influence model rather than the expected reward for staying of a reinforcement learning model. Related to Model-based analyses in the result part.



Extended figure 4. Overlap (in yellow) of brain regions correlating more with PE when trials are classified as competitive compared to those classified as cooperative (GLM2, in red), and of brain regions more coupled with the controller region at the time of choice of trials classified as Competitive compared to those classified as Cooperative (in green) (p<0.005 for display purpose)

References

- 780 1. Carter, R. M. K., Bowling, D. L., Reeck, C. & Huettel, S. A. A distinct role of the temporal-parietal junction in predicting socially guided decisions. *Science (80-.).* **336**, 109–111 (2012).
- 2. Bhatt, M. A., Lohrenz, T., Camerer, C. F. & Montague, P. R. Neural signatures of strategic types in a two-person bargaining game. *Proc. Natl. Acad. Sci. U. S. A.* **107**, 19720–19725 (2010).
- 3. Behrens, T. E. J., Hunt, L. T., Woolrich, M. W. & F.S., M. Associative learning of social value.

 Nature 456, 245–249 (2008).
- 786 4. Diaconescu, A. O. *et al.* Hierarchical prediction errors in midbrain and septum during social learning. *Soc. Cogn. Affect. Neurosci.* **12**, 618–634 (2017).
- 5. Suzuki, S., Adachi, R., Dunne, S., Bossaerts, P. & O'Doherty, J. P. Neural mechanisms underlying human consensus decision-making. *Neuron* **86**, 591–602 (2015).
- Hampton, A. N., Bossaerts, P. & O'Doherty, J. P. Neural correlates of mentalizing-related computations during strategic interactions in humans. *Proc. Natl. Acad. Sci. U. S. A.* **105**, 6741–6746 (2008).
- 793 7. Coricelli, G. & Nagel, R. Neural correlates of depth of strategic reasoning in medial prefrontal cortex. *Proc. Natl. Acad. Sci.* **106**, 9163–9168 (2009).
- 795 8. Hill, C. A. *et al.* A causal account of the brain network computations underlying strategic social behavior. *Nat. Neurosci.* **20**, (2017).
- Ogawa, A. & Kameda, T. Dissociable roles of left and right temporoparietal junction in strategic
 competitive interaction. *Soc. Cogn. Affect. Neurosci.* 14, 1037–1048 (2019).
- 799 10. Deutsch, M. A Theory of Competition and cCooperatioon. *Human Relations* **2**, 129–152 (1949).
- 800 11. Deutsch, M. Cooperation and trust: Some theoretical notes. in *Nebraska Symposium on Motivation*, 1962. 275–320 (Univer. Nebraska Press, 1962).
- 12. Thibaut, J. W. & Kelley, H. H. *The Social Psychology of Groups*. (Wiley, 1969).
- Devaine, M., Hollard, G. & Daunizeau, J. The Social Bayesian Brain: Does Mentalizing Make a Difference When We Learn? *PLoS Comput. Biol.* **10**, (2014).
- Camerer, C. F., Ho, T. H. & Chong, J. K. A cognitive hierarchy model of games. *Q. J. Econ.* 119, 861–898 (2004).
- 807 15. Mi, Q., Wang, C., Camerer, C. F. & Zhu, L. Reading between the lines: Listener's vmPFC simulates speaker cooperative choices in communication games. *Sci. Adv.* **7**, (2021).

- 809 16. Suzuki, S., Niki, K., Fujisaki, S. & Akiyama, E. Neural basis of conditional cooperation. *Soc.*
- 810 *Cogn. Affect. Neurosci.* **6**, 338–347 (2011).
- 811 17. Yoshida, W., Seymour, B., Friston, K. J. & Dolan, R. J. Neural mechanisms of belief inference
- during cooperative games. *J. Neurosci.* **30**, 10744–10751 (2010).
- 813 18. Fareri, D. S. & Delgado, M. R. Differential reward responses during competition against in- and
- out-of-network others. Soc. Cogn. Affect. Neurosci. 9, 412–420 (2014).
- 815 19. Seo, H., Cai, X., Donahue, C. H. & Lee, D. Neural correlates of strategic reasoning during
- 816 competitive games. *Science (80-.).* **346**, 340–343 (2014).
- 817 20. Lee, D., Conroy, M. L., McGreevy, B. P. & Barraclough, D. J. Reinforcement learning and
- decision making in monkeys during a competitive game. Cogn. Brain Res. 22, 45–58 (2004).
- 819 21. Coricelli, G. & Nagel, R. Neural correlates of depth of strategic reasoning in medial prefrontal
- 820 cortex. *Proc. Natl. Acad. Sci. U. S. A.* **106**, 9163–9168 (2009).
- 821 22. Lee, D., McGreevy, B. P. & Barraclough, D. J. Learning and decision making in monkeys during
- 822 a rock-paper-scissors game. *Cogn. Brain Res.* **25**, 416–430 (2005).
- 823 23. Abe, H. & Lee, D. Distributed Coding of Actual and Hypothetical Outcomes in the Orbital and
- Dorsolateral Prefrontal Cortex. *Neuron* **70**, 731–741 (2011).
- 825 24. Barraclough, D. J., Conroy, M. L. & Lee, D. Prefrontal cortex and decision making in a mixed-
- 826 strategy game. *Nat. Neurosci.* **7**, 404–410 (2004).
- 827 25. Vickery, T. J., Chun, M. M. & Lee, D. Ubiquity and Specificity of Reinforcement Signals
- 828 throughout the Human Brain. *Neuron* **72**, 166–177 (2011).
- 829 26. O'Doherty, J. et al. Why and how the brain weights contributions from a mixture of experts. 1–18
- 830 (2021). doi:10.31234/osf.io/ns6kg
- 831 27. Dorfman, H. M. & Gershman, S. J. Controllability governs the balance between Pavlovian and
- instrumental action selection. *Nat. Commun.* **10**, 1–8 (2019).
- 833 28. Wan Lee, S., Shimojo, S. & O'Doherty, J. P. Neural Computations Underlying Arbitration between
- Model-Based and Model-free Learning. *Neuron* **81**, 687–699 (2014).
- 835 29. Charpentier, C. J., ligaya, K. & O'Doherty, J. P. A Neuro-computational Account of Arbitration
- between Choice Imitation and Goal Emulation during Human Observational Learning. *Neuron*
- 837 **106**, 687-699.e7 (2020).
- 838 30. Zhu, L., Mathewson, K. E. & Hsu, M. Dissociable neural representations of reinforcement and
- belief prediction errors underlie strategic learning. *Proc. Natl. Acad. Sci. U. S. A.* **109**, 1419–1424
- 840 (2012).

- 31. Lee, D. & Seo, H. Neural Basis of Strategic Decision Making. *Trends Neurosci.* **39**, 40–48 (2016).
- Seo, H. & Lee, D. Behavioral and Neural Changes after Gains and Losses of Conditioned Reinforcers. *J. Neurosci.* **29**, 3627–3641 (2009).
- Schwieren, C. & Weichselbaumer, D. Does competition enhance performance or cheating? A laboratory experiment. *J. Econ. Psychol.* **31**, 241–253 (2010).
- 846 34. Bartolo, R. & Averbeck, B. B. Prefrontal Cortex Predicts State Switches during Reversal Learning. *Neuron* **106**, 1044-1054.e4 (2020).
- 35. Devaine, M., Hollard, G. & Daunizeau, J. Theory of mind: Did evolution fool us? *PLoS One* **9**, (2014).
- 850 36. Khalvati, K. *et al.* Modeling other minds: Bayesian inference explains human choices in group decision-making. *Sci. Adv.* **5**, eaax8783 (2019).
- 852 37. Rao, R. P. N. Decision Making Under Uncertainty: A Neural Model Based on Partially Observable 853 Markov Decision Processes. *Front. Comput. Neurosci.* **4**, 1–18 (2010).
- 854 38. Khalvati, K., Kiani, R. & Rao, R. P. N. Bayesian inference with incomplete knowledge explains perceptual confidence and its deviations from accuracy. *Nat. Commun.* **12**, 1–16 (2021).
- 856 39. Park, S. A., Sestito, M., Boorman, E. D. & Dreher, J. C. Neural computations underlying strategic social decision-making in groups. *Nat. Commun.* **10**, 1–12 (2019).
- Khalvati, K., Mirbagheri, S., Park, S. A., Dreher, J. C. & Rao, R. P. N. A Bayesian theory of conformity in collective decision making. *Adv. Neural Inf. Process. Syst.* **32**, (2019).
- 860 41. Rusch, T. *et al.* A Neuro-Computational Characterization of Theory of Mind Processes during Cooperative Interaction. 243–246 (2019). doi:10.32470/ccn.2019.1051-0
- Rusch, T., Steixner-Kumar, S., Doshi, P., Spezio, M. & Gläscher, J. Theory of mind and decision science: Towards a typology of tasks and computational models. *Neuropsychologia* **146**, 1–44 (2020).
- Mathys, C., Daunizeau, J., Friston, K. J. & Stephan, K. E. A Bayesian foundation for individual learning under uncertainty. *Front. Hum. Neurosci.* **5**, 1–20 (2011).
- 867 44. Friston, K. et al. Active inference and epistemic value. Cogn. Neurosci. 6, 187–224 (2015).
- 868 45. Rigoux, L., Stephan, K. E., Friston, K. J. & Daunizeau, J. Bayesian model selection for group studies Revisited. *Neuroimage* **84**, 971–985 (2013).
- 870 46. Rigoux, L. et al. Bayesian Model Selection for group studies. Neuroimage 46, 1004–1017 (2009).
- 871 47. Glover, S. & Dixon, P. The role of predictability in cooperative and competitive joint action. J.

- 872 Exp. Psychol. Hum. Percept. Perform. **43**, 644–650 (2017).
- 48. Hampton, A. N., Bossaerts, P. & O'Doherty, J. P. The Role of the Ventromedial Prefrontal Cortex
- in Abstract State-Based Inference during Decision Making in Humans. J. Neurosci. 26, 8360-
- 875 8367 (2006).
- 876 49. Schuck, N. W., Cai, M. B., Wilson, R. C. & Niv, Y. Human Orbitofrontal Cortex Represents a
- 877 Cognitive Map of State Space. *Neuron* **91**, 1402–1412 (2016).
- 878 50. Niv, Y. Learning task-state representations. Nat. Neurosci. 22, 1544–1553 (2019).
- 879 51. Baram, A. B., Muller, T. H., Nili, H., Garvert, M. M. & Behrens, T. E. J. Entorhinal and
- ventromedial prefrontal cortices abstract and generalize the structure of reinforcement learning
- 881 problems. *Neuron* **109**, 713-723.e7 (2021).
- 882 52. Rilling, J. K., Gutman, D. A., Zeh, T. R. & Pagnoni, G. A Neural Basis for Social Cooperation.
- 883 Neuron **35**, 395–405 (2002).
- 884 53. Suzuki, S. et al. Learning to Simulate Others' Decisions. Neuron 74, 1125–1137 (2012).
- 885 54. Vickery, T. J., Kleinman, M. R., Chun, M. M. & Lee, D. Opponent identity influences value learning
- 886 in simple games. *J. Neurosci.* **35**, 11133–11143 (2015).
- 887 55. Griessinger, T. & Coricelli, G. The neuroeconomics of strategic interaction. *Curr. Opin. Behav.*
- 888 *Sci.* **3**, 73–79 (2015).
- 889 56. Boorman, E. D., O'Doherty, J. P., Adolphs, R. & Rangel, A. The behavioral and neural
- mechanisms underlying the tracking of expertise. *Neuron* **80**, 1558–1571 (2013).
- 891 57. Behrens, T. E. J., Hunt, L. T. & Rushworth, M. F. S. The computation of social behavior. Science
- 892 *(80-.).* **324**, 1160–1164 (2009).
- 893 58. Domenech, P., Rheims, S. & Koechlin, E. Neural mechanisms resolving exploitation-exploration
- dilemmas in the medial prefrontal cortex. *Science (80-.).* **369**, (2020).
- 895 59. Donoso, M., Collins, A. G. E. & Koechlin, E. Foundations of human reasoning in the prefrontal
- 896 cortex. Science (80-.). **344**, 1481–1486 (2014).
- 897 60. Kim, D., Park, G. Y., O'Doherty, J. P. & Lee, S. W. Task complexity interacts with state-space
- uncertainty in the arbitration between model-based and model-free learning. *Nat. Commun.* **10**,
- 899 (2019).
- 900 61. Chung, Y. S., Barch, D. & Strube, M. A meta-analysis of mentalizing impairments in adults with
- 901 schizophrenia and autism spectrum disorder. *Schizophr. Bull.* **40**, 602–616 (2014).
- 902 62. Hampton, A. N., Bossaerts, P. & O'Doherty, J. P. Neural correlates of mentalizing-related

- computations during strategic interactions in humans. *Proc. Natl. Acad. Sci.* **105**, 6741–6746 (2008).
- 905 63. Mathys, C. D. *et al.* Uncertainty in perception and the Hierarchical Gaussian Filter. *Front. Hum.* 906 *Neurosci.* **8**, 1–24 (2014).
- 907 64. Mazaika, P. K., Hoeft, F., Glover, G. H. & Reiss, A. L. Methods and Software for fMRI Analysis of Clinical Subjects. *Neuroimage* **47**, S58 (2009).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

• SIRPJCD.pdf