

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-03855508v1

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

1	
2	Neurocomputational mechanisms engaged in
3	detecting cooperative and competitive intentions of
4	others
5	
6 7 8 9 10 11	R. Philippe ¹ , R. Janet ¹ , K Khalvati ² , R.P.N. Rao ^{2,3} , D Lee ⁴ , JC. Dreher ^{1*}
12	¹ CNRS-Institut des Sciences Cognitives Marc Jeannerod, UMR5229, Neuroeconomics, reward, and
13	decision making laboratory. 67 Bd Pinel, 69675 Lyon, FRANCE
14	² Paul G. Allen School of Computer Science and Engineering, University of Washington, 185 Stevens
15	Way, Seattle, WA 98195
16	³ Center for Neurotechnology, University of Washington, Seattle, WA 98195
17	⁴ The Zanvyl Krieger Mind/Brain Institute, Kavli Neuroscience Discovery Institute, Department of
18	Neuroscience, Department of Psychological and Brain Sciences, Johns Hopkins University, 3400 N.
19	Charles St, Baltimore, MD 21218, USA
20	
21	* Corresponding author
22	
23	
24	
25	
26	
27	
28	

29 Abstract

30 Humans frequently interact with other agents whose intentions can fluctuate over time between 31 competitive and cooperative strategies. How does the brain decide whether the others' intentions are 32 to cooperate or compete when the nature of the interactions is not explicitly signaled? We used model-33 based fMRI and a task in which participants thought they were playing with another player. In fact, this 34 agent was an algorithm alternating without signaling between cooperative and competitive strategies. 35 A neurocomputational mechanism underlying arbitration between competitive and cooperative experts 36 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 37 38 intentions, these regions increased their coupling with a network that distinguish prediction error related 39 to competition versus cooperation. These findings provide a neurocomputational account of how the 40 brain dynamically arbitrates between cooperative and competitive intentions when making adaptive 41 social decisions.

43 Introduction

44 During social interactions, humans are often uncertain whether others intend to compete or 45 cooperate. The intentions of other agents can fluctuate over time, making it challenging to develop 46 behavioral strategies. A key guestion is to understand how the brain decides whether the other is 47 cooperating or competing during volatile situations in which the nature of the social interactions is not 48 explicitly determined, as when others interact to achieve a common goal while maximizing their own 49 benefits. This guestion is of importance since it lies at the heart of strategic social decision making ^{1–9}. 50 In these types of situations, other agents can change behavior according to cooperative or competitive 51 intentions. Cooperation is generally defined as involving a group of individuals working together to attain 52 a common goal ^{10,11}. In contrast, competition involves one person attempting to outperform another in 53 a zero-sum situation ¹². A number of theoretical accounts and experimental results demonstrate that 54 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 55 intentions to others has been studied in situations in which participants are explicitly informed about the 56 nature of the interactions, either in a collaborative context alone ^{15–17} or in a competitive context alone 57 ^{8,18-25}. For example, during a cooperative game such as the coordination game, one of the best 58 59 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 60 61 equally often and randomly across trials. If the identity of the game played is not known, the agent has 62 to adjust his/her strategy based on repeated interactions with others and to infer 63 cooperation/competition on the basis of observations. How the brain achieves such inference poses a 64 unique computational problem because it not only requires the recursive representation of reciprocal 65 beliefs about other's intentions, as in cooperative or competitive contexts alone, but it also requires one 66 to decide whether the other is competing or cooperating to deploy an appropriate behavioral strategy.

67 Here, we sought to determine the neurocomputational mechanisms that underlie the inferences 68 of whether a person is competing or cooperating during volatile situations in which the nature of the 69 interactions is not explicitly signaled. A recent computational account proposed that arbitration between 70 strategies is determined by their predictive reliability, such that control over behavior is adaptively 71 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-72 free learning ²⁸ and learning by imitation or emulation ²⁹. Extending this concept of a mixture of experts 73 74 to social interactions, we investigated whether the brain relies on distinct experts to compute the best 75 choice between two possible intentions attributed to others (cooperation or competition) and then 76 weights them by their relative reliability. We tested and compared these mixtures of models, that 77 attribute intentions to others dynamically, with different classes of learning models: non-Bayesian vs 78 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.

81 The majority of theoretical frameworks used to model feedback-dependent changes in decision 82 making strategies, such as choice reinforcement and related Markov Decision Process (MDP) models, 83 assume that optimal decisions can be determined from the observable events and variables by the 84 decision makers. Clearly, these assumptions do not capture the reality and complexity of human social 85 interactions because observable behaviors of other individuals provide only very partial information 86 about their likely future behaviors. Moreover, model-free RL algorithms assume that values (utility or 87 desirability of states and actions), change incrementally across trials. This assumption is incorrect when 88 option values change abruptly, such as when the intention of the other shifts between cooperation and 89 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}. 90

91 A more accurate account of strategic learning is based on a family of RL models which adds a 92 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 93 94 proposes a basic form of mentalizing by having a representation of the other's strategy. Influence 95 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 96 97 models formalize not only how players react to others' past choices, (first-order beliefs in Theory of 98 Mind: ToM), but also how they anticipate the influence of their own choices on the others' behavior (i.e., 99 mentalizing-related second-order beliefs). Another modeling approach of theory of mind used Bayesian 100 algorithms to model inferences about the future actions of another, attempting to take their point of view 101 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 102 103 grounded in the theoretical framework of Partially Observable Markov Decision Processes (POMDPs) 104 ³⁶. POMDPs provide a probabilistic framework for solving tasks involving action selection and decision 105 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 106 competitive tasks where the intentions of players do not change over a given period^{13,35,41,42}. 107

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.

122 We found that the model accounting best for behavior was a mixture of influence models. 123 referred to as Mixed-Intention Influence Model. Two expert systems work together to make strategic 124 decisions, one assessing competitive intentions and the other assessing cooperative intentions, a 125 controller weighting between these experts according to their relative reliabilities. Each expert system 126 uses a classic RL algorithm complemented with a mentalizing term to infer the other's actions. This 127 Mixed-Intention Influence model accounts for behavior observed in naturalistic environments in which 128 the other's goal is often only partially congruent with one's own, allowing for a continuous range of 129 behavior between pure cooperation and pure competition. A brain network including the ventromedial 130 prefrontal cortex (vmPFC) and the ventral striatum tracked the reliability signal from the controller. This 131 finding indicates that the Mixed-Intention Influence model captures the higher-order structure of the 132 mixed-intentions task (i.e., alternation between cooperation and competition). When comparing trials 133 classified as competitive versus cooperative by the controller, we also identified a brain system engaged 134 with an updating signal used for learning. Finally, when participants expected higher utility for choosing 135 according to a competitive rather than cooperative strategies, the vmPFC and the ventral striatum, 136 tracked the intentions of others and showed changes in functional connectivity with a brain system 137 including the right temporo-parietal junction (rTPJ), dorsolateral prefrontal cortex (dIPFC) and the intra-138 parietal sulcus (IPS), which discriminates reward prediction error (PE) between believed modes of 139 interaction. Together, these results provide a model-based account of the neurocomputational 140 mechanisms guiding human strategic decisions during games in which the intentions of others fluctuate 141 between cooperation and competition.

143 **Results**

144 Behavioral signature of tracking intentions

145 We assessed how participants used the history of previous interactions to make their choices. 146 We used logistic regression to examine whether participants selected the same target as that from the 147 previous trial ("Stay") or chose the other target ("Switch"), depending on whether the previous three 148 trials (at t-1, t-2 and t-3) had been won or lost, whether the previous decisions had been to Stay or 149 Switch, and whether the previous interactions from those trials indicated cooperation (see below). We 150 also added sex, age and the number of trials as control variables. All trials except the 5 initialization 151 trials were included in this analysis. Cooperation was defined by a binomial variable, representing the 152 interaction between the last action of the Artificial Agent (AA) and the participant's own previous 153 outcome ("Cooperativity signature"). This variable was set to 1 if either the participant had won on the 154 previous trial and the AA stayed on the same target for the next trial, or if the participant lost on the 155 previous trial and the AA switched to the other target the trial just after. Otherwise, the variable was set 156 to 0. Indeed, from the perspective of the participant, if the AA is a cooperative partner, both players win 157 at the same time and should then choose to keep the same target to be more predictable.

158 We found that the "Cooperativity signature" predicted an increase in the "stay" probability of 159 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 160 161 tracked whether the other agent was cooperating during the two previous trials (but not before). 162 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**). 163

164

165 **Computational models tracking intentions of the other agent**

166 To elucidate the computations underlying strategic decision making, we compared the results 167 of different computational models. These models were split into five classes (see SI). The first class of 168 models, based on heuristics, included Win-Stay/Lose-Switch and Random Bias models. The other four 169 classes of algorithms can be classified into non-Bayesian versus Bayesian model families along one 170 dimension and mentalizing versus non-mentalizing model families along the other dimension. Thus, the 171 second class of models includes non-Bayesian, non-mentalizing models represented by reinforcement 172 learning (RL) models. The third class represents non-Bayesian mentalizing models, namely the 173 "influence models" which are RL models with an additional term representing how the actions of one 174 player influence those of the other player. The fourth class corresponds to Bayesian non-mentalizing 175 models, including (1) a Hierarchical Gaussian Filter (HGF) which tracks the volatility of outcome ⁴³, (2) 176 the k-Bayesian Sequence Learner which tracks the probability that one target will be selected by the 177 AA after a history of specific length k and (3) the active inference model which minimizes the expected 178 free energy ⁴⁴. The fifth class of models contains Bayesian mentalizing models, which are the *k*-ToM 179 models using recursive Bayesian inferences of depth *k* to predict the future choice of the AA. Each 180 mentalizing model was tested using 3 versions: a competitive, a cooperative and a 'mixed intentions' 181 version. The 'mixed intentions' version computes one decision value according to a competitive expert 182 and another according to a cooperative expert and arbitrates between the two, based on the difference 183 in their respective reliability (**see SI, Fig. 3a**). We defined reliability as the difference in unsigned value 184 functions for two choices given by particular learning algorithms.

185 Next, we performed a group-level random-effect Bayesian model selection on the models' 186 computed free energy, taking into account potential outliers and the number of free parameters ^{45,46}. 187 We found that the 'Mixed Intentions Influence Learning' Model was the most frequent best fit across the 188 population (Fig. 2b), demonstrating that subjects employed mentalizing-related computations in our 189 mixed intentions task. This finding also indicates that arbitration between a cooperative and a 190 competitive expert best explains most participants' behavior, rather than either expert taken individually. 191 Additionally, only the Mixed-Intention Influence model (and not the cooperative or the competitive one) 192 succeeded in producing behavior, similar to participants, with respect to the effect of the Cooperativity 193 signature on the probability to stay (Fig. 3b and Extended Fig.1, see SI). We conducted a logistic 194 regression to understand how the Mixed-Intention Influence model explained differences in behavioral 195 strategy to stay or switch target. This analysis included the reward prediction error at t-1, the valence 196 of the arbitration between cooperative and competitive intention at time t (sign(Δ); 1 for cooperative and 197 -1 for competitive), and the interaction between these two variables. This analysis revealed a main 198 effect of the valence of the arbitration (valence of the arbitration_t : estimate = 0.24, p < 0.0005, χ^2 199 test Fig. 3c) indicating that participant tend to stay more on the same target when they attributed 200 cooperative intention to the other. Moreover, we found an interaction effect, i.e. participants did not 201 integrate the prediction error in their strategy in the same way given the attributed intention 202 (valence of the arbitration_t * 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 203 204 when the controller attributed cooperative intentions compared to when it attributed competitive 205 intentions. In addition, we also performed another logistic regression analysis using the same variables 206 and the actual mode of interaction (i.e. competitive block trials versus cooperative block trials), rather 207 than the classified mode of interaction made by the controller. We did not find the same interaction 208 effect when we compared actual competitive and cooperative block trials (Block typet * rPE_{t-1} : estimate = 0.003, p = 0.56, Block type_t: estimate = 0.03, p = 0.229, and PE_{t-1} : estimate = 209 0.14, p < 0.0005, χ^2 test; **Extended Fig.2, see SI**), showing that the classified intentions, but not 210 211 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.

221 We hypothesized that repeated social victories should favor the attribution of cooperative 222 intentions because a series of victories suggests that both players are satisfied with the outcome. In 223 such situations the other player (i.e. AA) has become more predictable, which is an important feature 224 to build cooperation ⁴⁷. Moreover, the interaction between outcome and AA's choice (i.e. the tendency 225 of the AA to "stay" after a participant wins or "switch" after a participant loses) should drive the arbitrator 226 to favor the cooperative mode, because playing the same winning target for both players corresponds 227 to the optimal Nash equilibrium of the cooperative game. To test this hypothesis, we regressed the 228 signed difference in reliability on (1) the participant's last outcome, (2) AA's choice to "stay" or to "switch" 229 and (3) the interaction between the participant's outcome and the AA's choice to stay or switch 230 (Cooperativity signature) over up to three retrospective trials. We found that the past two interactions 231 between participant's outcome and AA's action (Cooperativity signature), the last outcome and switches 232 AA t-2 t-3 explained by the at trial and the difference in reliability 233 (*Cooperativity signature* $_{t-1}$: *estimate* =0.59, p<0.0005; 234 *Cooperativity signature* $_{t-2}$: *estimate* =0.06, p=0.037; *Victory*: *estimate* = **1.98**, 235 p<0.0005; switch $_{t-2}$: estimate =-0.18, p<0.0005; switch $_{t-3}$: estimate =-0.07, p<0.0005), χ^2 test, 236 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**).

242

243 Model-based fMRI analyses

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 249 reward prediction error as a parametric regressor at the outcome time and we controlled for the other's 250 intention effect by adding Δ as a non-orthogonalized regressor. The bilateral ventral striatum 251 (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 252 middle cingulate cortex (MCC; x,y,z=11,-15,57, p<0.05 whole-brain family-wise error (FWE), Fig. 4b 253 and 4c) tracked the difference in reliability between experts (Δ) at the decision time. Bilateral dorsal 254 striatum (DS; x,y,z=17,6,-12 and -14,3,-11), bilateral orbitofrontal cortex (OFC; x,y,z=44,36,-14 and -44 255 52 8), posterior cingulate cortex (PCC; x,y,z=2,-34,38), and bilateral angular gyrus (x,y,z=45,-30,46 and 256 -54,-62,39) (p<0.05 FWE, Fig. 5a) encoded the reward prediction error at the outcome time.

257 To investigate brain areas encoding the reward prediction error that were more engaged when 258 the controller classified a trial as competitive vs cooperative, we tested another GLM (GLM2). Trial 259 onsets were separated according to whether the value of the signed reliability difference Δ added to the 260 bias was positive or negative. If this value was ≥ 0 , the trial was classified as Cooperative, and 261 Competitive otherwise. The computed expected reward for staying on the same target was used as a 262 parametric regressor at the time of choice. We found that the right dIPFC (x,y,z=35,11,36), the IPS 263 region (x,y,z=50,-50,32) and the right temporoparietal junction (rTPJ; x,y,z = 51,-50,33, p<0.05 FWE) 264 were more engaged in encoding reward prediction error in trials classified as Competitive versus 265 Cooperative (p<0.05, FWE Fig. 5b and 5c). This effect could not be explained by less variance in the 266 PE regressor in trials classified as Competitive trials compared to those classified as Cooperative, 267 because we observed no difference in regressor variance on these two types of trials (p=0.57, Levene's 268 test). No region was more engaged in trials classified as Cooperative compared to those classified as 269 Competitive.

270 To further investigate the relationship between the behavior to stay after a trial classified as 271 Competitive versus classified as Cooperative and the BOLD signal, we conducted a logistic regression. 272 Explanatory variables were the average of the weighted time series in the dIPFC and rTPJ/IPS region 273 observed in GLM2, the valence of the controller (Δ) and their interactions. This signal was extracted at 274 the time of the outcome and convolved with the hemodynamic function. Because there was an average 275 of 6.6 scans per trial, we took as a predictor variable the mean of this weighted signal through the 7 276 scans following the outcome presentation. We found an interaction between the weighted time series 277 and the valence of the arbitration (valence of the arbitration_t * weighted time series_{t-1} : estimate = 278 -14.4, p = 0.0312, χ^2 test). Post hoc tests further revealed that this effect was driven by trials classified (weighted time series_{t-1} of trial classified as competitive_{t-1} : estimate = 279 as Competitive -37.3, p = 0.040, χ^2 test). This result indicates that activation of rdIPFC and rTPJ/IPS increases the 280 probability of switching following a trial classified as Competitive. 281

282

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

284 **Connectivity analysis**

285 Finally, we performed a generalized psycho-physiological interaction (gPPI) seed to voxels 286 connectivity analysis to understand the interactions between brain regions tracking the arbitration 287 process (i.e. Δ : reliability difference) for the cooperative and competitive experts and those more 288 engaged with the PE when the controller attributes more competitive than cooperative intentions to the 289 other (see Online Methods). We used the ventral striatum and vmPFC, which encoded the controller, 290 as seed regions (ROI extracted from the GLM1 striatal and vmPFC activity) for trials classified as 291 competitive compared to those classified as cooperative (i.e. trials for $\Delta < 0$ or $\Delta > 0$) at the decision time. 292 We found stronger functional connectivity between regions encoding the difference in reliability and the 293 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, 294 p<0.05 FWE: Fig. 6a) at the decision time for trials classified as Competitive compared to those 295 classified as Cooperative. This result indicates that the dIPFC, IPS and left TPJ receive an input signal 296 at the time of choice according to the difference in reliability with respect to the Competitive versus 297 Cooperative believed intention of others. This brain network largely overlaps with the brain network 298 observed with the PE differentiating between trials classified as Competitive versus Cooperative at the 299 outcome (Fig. 5b and Extended Fig. 4).

301 Discussion

302 To make a strategic decision when facing an individual with unknown and fluctuating intentions. 303 it is necessary to make inferences as to whether we are in a competitive or cooperative situation. In the 304 context of minimal information, for example when only the choices of the other, but not their outcomes, 305 are available, such inferences are much more difficult than when one is in a specific known setting (e.g., 306 in a competitive game) ¹⁹. Here, we provide evidence that the brain engages in dynamic tracking of 307 another individual's cooperative/competitive intentions, despite having no explicit information regarding 308 whether the situation is cooperative or competitive. We found that strategies of participants were mostly 309 affected by the outcomes of previous interactions and by a "signature" of the other's cooperativity, i.e. 310 the tendency of the other (here the Artificial Agent or AA) to stay on the same target after the 311 participant's winning. Comparison between computational models demonstrated that such behavior is 312 best explained by a model in which choice is driven by a controller tracking the reliability difference 313 between cooperative and competitive intentions. The fMRI results show that the neural computations 314 of this controller are implemented in the ventral striatum and in the vmPFC. Thus, both behavior and 315 brain imaging results can be accounted for by a model that includes a controller that allocates resources 316 according to different experts' predictions. At the time of outcome, a common brain network, including 317 the rostral anterior cingulate cortex (rACC), ventral striatum and lateral OFC encoded prediction error 318 in trials classified as Competitive or as Cooperative. However, prediction error signals in some brain 319 areas also depended on the classification of the current trial as Cooperative or Competitive as classified 320 by the controller. That is, a distinct brain network, composed of the bilateral dIPFC, bilateral IPS regions 321 and the rTPJ was more engaged for trials classified as Competitive compared to those classified as 322 Cooperative. This latter brain network reflects a differential use of the outcome of the social interaction 323 as a function of whether it is classified as Competitive or Cooperative (Fig. 2d).

324 Mentalizing processes are essential to correctly infer the strategy of others. This is true in the 325 cooperative context, in which participants performed above chance, reflecting their ability to effectively 326 infer the other's (i.e. AA's) behavior. In the competitive context, participants performed below chance 327 level, showing that the AA was able to predict their behavior and to exploit their previous 328 choices/outcomes. The Mixed-Intention Influence model had the best ability to predict data and to 329 generate very similar behavior to the participants. Each expert model is an expanded RL model, with a 330 term accounting for one's previous choice influencing the choice of the other. Although only the 331 influence term differed between the Competitive and Cooperative models, the Mixed-Intention Influence 332 model tracked intentions based on this second order mentalizing term by weighting the contribution of 333 a cooperative and of a competitive expert. One key aspect of this Mixed-Intention Influence model is 334 that it captures higher order structures (fluctuations between cooperation and competition) during social 335 interactions. In contrast, one important limitation of the classical RL model is that it does not exploit 336 higher-order structures such as interdependencies between different stimuli, actions, and subsequent 337 rewards. Previous studies demonstrated that models incorporating such structures can account for 338 individual decision making in different situations ^{48–51}. Here, we demonstrate that the representation of 339 abstract states, such as whether the other is cooperating or competing, can be extended to social 340 decisions and underlies the ability to build strategies. To confirm that the Mixed-Intention Influence 341 model accounted more for neural activity in brain areas involved in social interactions, we formally 342 compared the brain regions covarying more with the expected reward for staying on the same target, 343 as computed by the winning model, compared to the expected reward for staying on the same target, 344 computed by a simple RL model (Extended Fig. 3). One crucial difference between a simple RL model 345 and the Mixed-Intention Influence model is that in the former, only the value of the chosen option is 346 updated and the valuation of the option that was not chosen does not change. In the latter, both the 347 values of the chosen and unchosen options are updated to incorporate the knowledge that the current 348 state has a given reliability to be cooperative or competitive. The controller weights the valuation 349 produced according to the competitive or cooperative hypothesis which is computed as a sigmoid of 350 the difference in reliability between the two experts.

351 Activity in the ventral striatum and vmPFC increased as the cooperative prediction from the 352 controller became more reliable than the competitive prediction, as a result of the outcomes of the 353 previous interactions (reliability difference modulated by last outcome) and the other's "Cooperativity 354 signature" over the last trials. Thus, these brain regions dynamically track the reliability difference 355 between intentions classified as cooperative and competitive in a situation where the nature of the social 356 interactions is implicit. Previous reports demonstrated a role of the ventral striatum when making 357 cooperative choices alone, in response to a partner's cooperative choice in an explicit cooperation task 358 ⁵² and also in the attribution of intentions in a competitive context ³⁰. Our findings show that strategic 359 social behavior can be explained by a Controller Theory according to which cooperative/competitive 360 social behavior results from the interaction of multiple systems, each proposing possible strategies for action 26,28,29. 361

362 One strength of our computational approach was to assess and compare a large variety of 363 competing models, (active inference, recursive learning models k-TOM and a mixture of experts using 364 k-TOM, influence models for only cooperative strategies or competitive strategies, a mixture of experts 365 using influence models, fictitious learner, Bayesian Sequence learner, Hierarchical Gaussian Filter, 366 Reinforcement Learning and Heuristic models). Many have never previously been directly tested 367 against each other. Our results agree with studies concluding thatsocial learning may be driven by nonspecific reinforcement processes that include a mentalizing term ^{3,6,8,30,53}. We demonstrate that when a 368 369 task is not explicitly signaled as cooperative or competitive, this evokes the arbitration between 370 strategies determined by predictive reliability. Behavior is hence controlled by giving a higher weight to 371 the strategy with the most reliable prediction ²⁹. At first glance, it may be surprising to observe that the 372 mixture of expert influence models performs better than mathematically more sophisticated models,

373 such as POMDP models (HGF, active inference, k-ToMs) and models mimicking different levels of 374 mentalizing (k-TOM). However, this is likely because in our setting the only information that can be 375 integrated by participants is their own choices, rewards and the history of the choices made by the other 376 (i.e. AA). The nature of the social interaction is never explicitly signaled (participants are not told whether 377 the other is cooperative or competitive), and the rewards of the other are not observed. This uncertainty 378 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 379 380 investigated learning of social interactions in either competitive or cooperative situations alone 381 (matching-pennies or rock-paper-scissors games against computerized opponents)^{25,54}. Our findings 382 also broadly agree with a cognitive hierarchy of strategic learning mechanisms, proposing that distinct 383 levels of strategic thinking correspond to different levels of sophistication of learning mechanisms (in 384 increasing order of complexity: reinforcement learning, fictitious play learning and influence learning) 385 ⁵⁵. However, we propose a more general model based on a mixture of influence learning experts that 386 function in parallel and are then compared with respect to their relative reliability.

387 Competitive social interactions often emerge in situations where an agent's outcome depends 388 on the choices of others, which requires the ability to infer the intentions of others ⁶. In the context of 389 our mixed intentions task, when participants attributed competitive, as opposed to cooperative 390 intentions to others, the dIPFC and rTPJ/IPS specifically encoded a relative PE. Although this network 391 has previously been reported when inferring the intentions of others ^{8,39,56}, the strength of our 392 computational account of theory of mind processes is to specify that this brain network computes a PE 393 difference between trials that the controller classified as competitive versus cooperative. This PE 394 difference reflects a differentiation in the implementation and use of the outcome of the social interaction 395 as a function of the classified interaction (Fig. 3c). Note that PE was not more volatile in trials when the 396 competitive expert is more reliable than the cooperative expert. This rules out the possibility that the 397 observed PE difference reflects higher PE volatility in competitive contexts. When comparing intentions 398 classified as cooperative compared to competitive, participants tended to be more predictable, staying 399 more on the same target after experiencing an unexpected social defeat (i.e. after higher negative PE) 400 (Fig. 3c). This behavior likely reflects a signal sent to the other to indicate one's willingness to stay on 401 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 402 403 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 (dIPFC, 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). 409 This reflects a differential use of the outcome of the social interaction as a function of whether it is 410 classified as Competitive or Cooperative. Thus, according to the attributed intention of other by the 411 controller, PE signals differed and the strength of functional coupling increased between regions 412 encoding the reliability difference of the controller and the dIPFC-TPJ network. When one expert is 413 more reliable than the other, the Mixed-Intention Influence model predicts that the reward PE is driven 414 by the valuation of the more reliable expert. Since the only difference between experts is the sign of the 415 second-order mentalizing term, this suggests that the implication of the dIPFC-TPJ network at the 416 outcome is engaged when there is a need to mentalize intentions of other agents with opposing goals 417 (i.e. intentions classified as Competitive). Moreover, engagement of the dIPFC-TPJ network increases 418 the probability of switching following a trial classified as competitive by the controller, allowing 419 behavioral adaptation by virtue of the reliability difference signal.

420 Together, our work provides evidence that the mixture of experts model explains behavior in 421 socially volatile situations differing only by the reward function of other agents. These two experts only 422 differ by their priors on how their reward function takes into account another agent's reward (i.e. the 423 second order mentalizing term), and were sufficient to discriminate the others' intentions. These findings 424 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 425 426 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" 427 systems ^{26,28,60} and learning by imitation vs emulation ²⁹. Finally, our Mixed-Intention Influence model 428 429 may be useful in the field of computational neuropsychiatry to identify the specific computational 430 components that are modified in theory of mind alterations, a key feature of autism spectrum disorder 61 431

433 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.

439

440 Acknowlegements

441 This research has benefited from the financial support of IDEXLYON from Université de Lyon 442 (project INDEPTH) within the Programme Investissements d'Avenir (ANR-16-IDEX-0005) and of the 443 LABEX CORTEX (ANR-11-LABX-0042) of Université de Lyon, within the program Investissements 444 d'Avenir (ANR-11-IDEX-007) operated by the French National Research Agency. This work was also 445 supported by grants from the Agence Nationale pour la Recherche and NSF in the CRCNS program to 446 JCD (ANR n°16-NEUC-0003-01), and by CRCNS NIMH grant no. 5R01MH112166-03, NSF grant no. 447 EEC-1028725, and a Templeton World Charity Foundation grant to RPNR.. We thank the CERMEP 448 Staff for help during scanning and Pr Ed Derrington for proof reading the draft of the manuscript.

449

450 Competing interests

451 The authors declare that they have no competing interests.

452

453 **Resources availability**

454 Lead contact

455 Further information and requests for resources and inquiries should be directed to and will be 456 fulfilled by the lead contact, Jean-Claude DREHER (dreher@isc.cnrs.fr).

457 This study did not generate new unique reagents.

458 Materials availability

459 This study did not generate new unique reagents.

460 Data and code availability

461	Code	supporting	main	results	are	available	at	GitHub
462	(https://github.cc	om/remiphilipp/Mi	xture_inten	tion.git).				

463 **Method**

464 **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.

471 Mixed intentions task

472 Participants performed a novel task comprising 163 trials in an MRI scanner. They were led to 473 believe that they were interacting with another person via a computer interface, while in fact they were 474 playing against an artificial agent (AA) managed by a computer program. Such simulated social 475 interactions allowed us to investigate the dynamics and neural mechanisms arbitrating between multiple 476 learning algorithms. Participants were faced with a screen containing four cards, two face down (the 477 other player's cards) and two face up (their own cards). Participants were informed that to win, they had 478 to choose the card of the same color as the one the other person was going to choose. Experimenters 479 were careful not to specify whether the other was an adversary or a partner. Participants were told that 480 they and the other player had to make their choices in four seconds (Fig. 1a). If the Artificial Agent (AA) 481 played before the participant, one of the two face down cards was removed from the playing field. If the 482 participant chose first, only the selected card remained on the playing field. Then, when both had 483 chosen, the chosen cards were revealed and the participant received a reward if the card colors 484 matched, otherwise they received nothing. Participants were led to believe that their final payoff would 485 be increased by 10 ct (euro) for each winning interaction. No information about the other's payoff was 486 given to the participants, they only knew that after an interaction, the other 'participant' would see the 487 same screen but with their outcomes which could be different from the participant.

488 Importantly, unbeknownst to the participants, the artificial agent alternated between Competitive 489 and Cooperative trial blocks. During this mixed intentions task, the AA's strategy was determined by 490 alternating 13 trials of a hide and seek (HS) task (Competitive blocks), and 10 trials of a coordination 491 game (Cooperative blocks). The artificial agent algorithm was designed to predict the color that would 492 be chosen by the participant on the basis of a probabilistic analysis of the two previous choices and 493 outcomes (see SI for the algorithm). Here we defined a competitive choice, made by the AA, as 494 choosing the card of the color the participant was expected not to play and a cooperative choice as 495 choosing the card with the same color. Thus, the artificial agent exploited the bias of the participants in 496 a stochastic way, i.e. the more predictable the participant was, the more the algorithm made correct 497 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 coloras that chosen by the other player (i.e. the AA).

500 The HS task is competitive, and the computer uses the record of the participant's choice and 501 reward history to minimize the participant's payoff. Therefore, in this case the subject's optimal strategy 502 during the HS task is to choose the two targets equally often and randomly across trials. During the 503 coordination game, the AA tried to maximize the subject's payoff and in this case the subjects should 504 try to choose one of the two targets consistently so that the computer can choose the same target as 505 them. Since the participant is not informed of either the goals of the AA or the switches between blocks. 506 they must adjust their strategy based on recent experience and infer cooperation/competition on the 507 basis of their observations.

508 This task was to designed to identify key components of the estimation of intentions regarding 509 whether others are cooperating or competing. We took advantage of the fact that an individual's 510 estimates as to whether they are engaged in a cooperative or competitive interaction can be assessed 511 even when the individual is interacting with a computer program rather than another person. Transitions 512 between the competitive and cooperative blocks were unsignaled, therefore subjects had to discover 513 by trial and error the most successful strategy over consecutive blocks. This alternation between the 514 two interaction modes functioned well because the participant's winning rate was significantly higher in 515 cooperative (mean 60% std 1%) than in competitive (mean 44% std 1%) trials (paired t-test $p < 10^{-4}$).

516

517 Artificial agent

518 The AA calculated the probability p for the participant to select a particular target color based on 519 the history of the two previous choices and their outcomes. Then to make the artificial agent behave 520 more like a real person, this prediction was exploited in a probabilistic fashion (**see SI**). In the 521 cooperative mode the AA chose the color card it predicted with probability p. In the competitive mode 522 this color was chosen with probability 1-p.

523

524 Behavioral analysis

525 For the logistic regressions, we reported significant marginal effect of a given variable under the 526 name "*estimate*" (for example: *Cooperativity signature* $_{t-1}$: *estimate*).

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

528 X_i represents independent variables and x_i represents the associated weights in the logistic 529 regression. *P* represent the probability of a given event. The marginal effect of the variable X_1 is defined 530 as:

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

532 The mean is computed across all observed data. Thus, the marginal effect called "*estimate*" can 533 easily be interpreted as the discreet change of the dependent variable given a unitary change of an 534 independent variable.

535 For the linear regressions, reported "*estimate*" represents x_i i.e. the regression coefficient. 536 Indeed, in a linear regression, marginal effect of a variable is equal to the estimated coefficient.

537 Models

538 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 539 on aylor expanded reinforcement learning ⁶² to take into account the influence of one's own strategy on 540 541 the strategy of the other. k-ToM models also take into account the influence of one's own strategy on 542 the other but in a Bayesian fashion ^{13,35}. These two models were adapted in their cooperative and 543 competitive versions. Moreover, we constructed an adaptation of these two models (*Inf,k-ToM*) in which 544 an arbitrator weights the cooperative and competitive versions according to their reliability before 545 making the decision. Finally, because k-ToM is a recursive model ("I think that you think that...), we 546 included k-ToM of depth one and two for each version.

547 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 548 549 tracks the external volatility of the artificial agent choices in a Bayesian hierarchical way. The Bayesian 550 Sequences Learner (BSL) strategy relies on Bayesian inference given past sequences of choices. In a 551 model free analysis, we found that participants tended to use the past 2 choices to make their next 552 choice, so we used sequences of depths 2 and 3. Finally, we added two non-Mentalizing non Bayesian 553 models, a reinforcement learning model (RL) and a model based on the heuristic Win/stay -554 Lose/Switch that we observed in the model free analysis.

555 The Bayesian Model Selection (BMS) was performed using the VBA toolbox (Variational 556 Bayesian Analysis) in a random effect analysis relying on the free energy as the lower bound of model 557 evidence. We use protected Exceedance Probability measurements (pEP) ⁴⁵ to select the model which 558 is used most frequently in our population.

559

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.

565

566 fMRI data acquisition

567 MRI acquisitions were performed on a 3 Tesla scanner using EPI BOLD sequences and T1 568 sequences at high resolution. Scans were performed in a Siemens Magnetom Prisma scanner 569 HealthCare at CERMEP Bron (single-shot EPI, TR / TE = 1600/30, flip angle 75°, multiband acquisition 570 (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 highresolution T1-weighted structural scans ($0.8 \times 0.8 \times 0.8 \text{ mm}$) were acquired for each subject, coregistered 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.

578

579 fMRI data analysis

580 Image analysis was performed using SPM12 (Wellcome Department of Imaging Neuroscience, 581 Institute of Neurology, London, UK, fil.ion.ucl.ac.uk/spm/software/spm12/). Time-series images were 582 registered in a 3D space to minimize any effect that could result from participant head-motion. Once 583 DICOMs were imported, functional scans were realigned to the first volume, corrected for slice timing 584 and unwarped to correct for geometric distortions. Inhomogeneous distortions-related correction maps 585 were created using the phase of non-EPI gradient echo images measured at two echo times (5.20 ms 586 for the first echo and 7.66 ms for the second). Finally, in order to perform group and individual 587 comparisons, they were co-registered with structural maps and spatially normalized into the standard 588 Montreal Neurological Institute (MNI) atlas space using the DARTEL method. Then we ran ARTrepair 589 to deweight scans that could include movement artefacts ⁶⁴.

590 We ran general linear models (GLMs) analyses to identify which brain regions encoded: (a) 591 one's belief that one is interacting in a cooperative or in a competitive situation (Δ); (b) the reward 592 prediction error (PE) after interactions classified as cooperative or competitive: (c) the PE difference 593 between the trials classified as cooperative vs competitive. In every GLM, an event was defined as a 594 stick function. The participant's button press and the AA's selection of target were defined as onset of 595 no interest in all GLMs. For all GLMs, missing trials were modeled with four events (cue, participant's 596 button press, AA's choice and outcome) as separate onsets without additional parametric regressors. 597 Head movement parameters were added as parametric regressors of no interest to account for motion-598 related noise. Because the behavioral analysis showed that the bias towards competitive interaction 599 affects the strategy of participants, we added the competitive bias (δ) as a covariate at the second level 600 analysis in all GLMs.

601 Specifically, in GLM1, there were 4 onsets, including the time of the cue presentation (cards on 602 screen), participant's button press, AA's choice and the feedback time. Parametric regressors were the 603 difference in reliability Δ , the expected reward for staying at the time of the cue onset and the reward 604 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 functionof regressors to allow it to compete for the variance.

607 In a second GLM (GLM2), we separated trials given the sign of Δ - δ (positive or negative) to 608 identify brain regions specifically engaged in cooperative or competitive mental states (δ is a free 609 parameter capturing the participant's bias toward competitive intent). Δ refers to the difference in 610 reliability of cooperative and competitive prediction and δ is the competitive bias. For this GLM, there 611 were 6 onsets, including the cue for trials classified as cooperative or competitive, participant's button 612 press, AA's choice and the feedback time for trials classified as cooperative or competitive. Trials were 613 classified as either cooperative or competitive and parametric modulators were: the difference in 614 reliability Δ and the expected reward for staying on the same target at the time of the cue and the PE 615 and Δ at the time of feedback. Three participants who always attributed the same intention to the AA 616 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 $\Delta - \delta$. 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.

627 We computed one sample t-tests with contrasts for main effect of Δ in GLM1 and effect of PE at 628 the outcome time. Then we computed the contrast between competitive and cooperative PE regressors 629 in GLM2, GLM3 and GLM4. Finally, we computed a paired t-test between this contrast, derived from 630 GLM2 and GLM3, to formally show that activation coming from the difference between classified trials 631 was significantly higher than those coming from the difference between the actual modes of interaction 632 as determined by the trial block.

633 Reported brain areas show a significant activity at the threshold of p<0.05, whole brain family-634 wise error (FWE), corrected for multiple comparisons at the cluster level (threshold at P<0.001 635 uncorrected).

637 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.

645 Reported brain areas show a significant activity at the threshold of p<0.05, whole brain family-646 wise error (FWE) corrected for multiple comparisons at the cluster level (threshold at P<0.001 647 uncorrected).

649 Figures

650



651

652 Figure 1. fMRI experiment. a. After a fixation cross, four cards were presented on the screen. The two 653 cards shown on top of the screen represent the cards presented to the opponent/partner (i.e. Artificial 654 agent), and not seen by the participant while the two kings (one black and one red) are the cards 655 presented to the participant (shown in the bottom of the screen). The participants had to choose 656 between these two cards. At the time of decision, the upper screen represents the display if the AA 657 makes it choice first, while the lower screen shows how one card is highlighted with yellow border if the 658 participant makes his choice first. Then a screen presents the participant's and Artificial Agent's choices 659 together. Finally, at the time of outcome the participant wins if both he/she chooses the same card as 660 the AA (here red king). b. Payoff matrix of the two types of block. c. Frequency of winning (black line) 661 during competitive (red background) and cooperative (green background) blocks. The grey area 662 represents the 95% confidence interval. The orange background represents 5 initial trials in which the 663 AA played randomly for initialization purpose.



667 Figure 2. a. Model-free analysis. Random-effect logistic regression of the decision to stay after 668 selecting a specific target with respect to the action of the artificial agent "Cooperativity signature" (i.e. 669 participant wins then AA stays or participant loses then AA switches), the previous winning interaction 670 (i.e. success or failure of past trials) and the choice to switch or stay, over the previous three trials. Error 671 bars are the 95% confidence interval. b. Model comparisons based on Bayesian model selection. The 672 protected exceedance probabilities indicate that the Mixed-Intention Influence model (Inf 2 expert) 673 explains decisions in the mixed intention task better than others: Active inference; k-ToM; Bayesian 674 Sequence Learner (BSL); Hierarchical Gaussian Filter (HGF); Reinforcement Learning (RL); Heuristic 675 models: Random Bias (RB); Win/Stay-Lose/Switch (WSLS).



679 Figure 3. a. Scheme of the Mixed-Intention Influence model. Two influence models (one cooperative 680 and the other competitive) compute a value for choosing one specific target (the black one). A controller 681 uses the difference between the absolute value of the value of each expert (called reliability) to compute 682 a probability that the other is cooperating. Then, the model weights the value of each expert according 683 to the probability of being in cooperative and in competitive modes to produce a final decision value. 684 Then it compares its predictions to the actual reward and compute again a new value for each expert. 685 b. Model-free generative analysis. We generated one hundred sets of data using a free parameter from 686 a normal distribution with mean and standard deviation calculated from the models fitted to the 687 population, against the same artificial agent that participants played. We regressed the behavioral 688 decision to stay after selection of a specific target on the previous trial depending on the interaction of 689 the previous outcome and the action of the artificial agent ("Cooperativity signature"), the success or 690 failure of up to three previous trials, and the action to switch or stay of the participant. Error bars are 691 the 95% confidence interval (random-effect logistic regression). c. Marginal effect of the prediction error 692 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 < 693 694 0.001 (random-effect logistic regression).

695

677



697 Figure 4. a. Difference in reliability is influenced by the Cooperativity signature of the Artificial Agent 698 (AA), specifically the interaction of the previous subject's outcome followed by the action of the artificial 699 agent (Participant wins then AA stays and Participant loses then AA switches), the latest outcome and 700 the computer's switch at trial t-2 and t-3. Error bars are the 95% confidence interval. b. Mean probability 701 of the participant attempting to cooperate across all participants (black line) for the 163 trials. The initial 702 orange area is the 5 random initializing trials, green areas are the Cooperative blocks and red areas 703 the Competitive blocks. The grey area is the 95% confidence interval. c. BOLD signal in ventral striatum, 704 mPFC and posterior cingulate cortex (PCC) (p < 0.05 whole-brain family-wise error) are correlated with 705 the difference in reliability, Δ , of estimated competitive and cooperative intentions.



708 Figure 5. Correlations between BOLD activity and prediction error. a. Brain regions in which BOLD 709 signal correlates with prediction errors for trials classified by the controller to be either competitive or 710 cooperative. b. Brain regions in which BOLD activity correlates more with PE on trials estimated to be 711 competitive compared to trials estimated to be cooperative. This network comprised dIPFC (x,y,z =712 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). 713 c. Beta value extracted for trials estimated to be either competitive or cooperative. Left: regions in the 714 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 715 activation in trials estimated to be either competitive or cooperative. Right: specific brain regions 716 activated only when trials were classified as Competitive: dIPFC (x,y,z = 30,9,42), IPS (x,y,z = 42,-717 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.

729 Extended data

730 Extended table

731

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

-							
	MNI peak cluster coordinates						
	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							

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

No brain region

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

733

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

	MNI peak cluster coordinates								
	x y 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				

Negatively

No brain region

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

737

739 Extended results table of GLM2, related to **Figure 5c.**

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								
x y 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.**

dIPFC/TPJ connectivity strength.									
gPPI Analyse Seed		Peak regions	k	p-val unc.	p-val FWE	Z score			
	mPFC + striatum	-48 -44 58	363	<0.0005	<0.0005	4.52			
Competitive >	mPFC + striatum	-2 -82 -36	153	<0.0005	0.037	4.34			
Cooperative	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			

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



746 Extended figure 1. Model-based generative analysis. We generated one hundred sets of data using 747 free parameters from a normal distribution with mean and standard deviation calculated from the 748 "Influence models" in competitive (a) and cooperative (b) mode, fitted to the population. We generated 749 a data set against the same artificial agent that participants played. We regressed the interaction of the 750 previous outcome and action of the artificial agent (I win – AA stay / I lose – AA switch), the behavioral 751 decision to stay after selecting a specific target at the previous trial based on the success or failure of 752 the previous trial (Win) and the action to switch or stay of the artificial agent (Switch) in previous trials 753 up to three trials back. Error bars are the 95% confidence interval. *p < 0.05, **p < 0.01, ***p < 0.001 754 (random-effect logistic regression). Related to Computational models tracking intentions of the other 755 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.



Mixed influence model > RL

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

- 779
- 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).
- 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).
- 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
 787 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
 794 cortex. *Proc. Natl. Acad. Sci.* 106, 9163–9168 (2009).
- Hill, C. A. *et al.* A causal account of the brain network computations underlying strategic social
 behavior. *Nat. Neurosci.* 20, (2017).
- 9. Ogawa, A. & Kameda, T. Dissociable roles of left and right temporoparietal junction in strategic
 competitive interaction. *Soc. Cogn. Affect. Neurosci.* 14, 1037–1048 (2019).
- 10. Deutsch, M. A Theory of Competition and cCooperatioon. *Human Relations* **2**, 129–152 (1949).
- Bou 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).
- Bos 13. Devaine, M., Hollard, G. & Daunizeau, J. The Social Bayesian Brain: Does Mentalizing Make a
 Difference When We Learn? *PLoS Comput. Biol.* 10, (2014).
- 805 14. Camerer, C. F., Ho, T. H. & Chong, J. K. A cognitive hierarchy model of games. *Q. J. Econ.* **119**,
 806 861–898 (2004).
- 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).
- 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
 814 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).
- 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).
- Lee, D., McGreevy, B. P. & Barraclough, D. J. Learning and decision making in monkeys during
 a rock-paper-scissors game. *Cogn. Brain Res.* 25, 416–430 (2005).
- 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 mixed826 strategy game. *Nat. Neurosci.* 7, 404–410 (2004).
- Vickery, T. J., Chun, M. M. & Lee, D. Ubiquity and Specificity of Reinforcement Signals
 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/ns6kq
- Borfman, 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
 834 Model-Based and Model-free Learning. *Neuron* 81, 687–699 (2014).
- Charpentier, C. J., Iigaya, K. & O'Doherty, J. P. A Neuro-computational Account of Arbitration
 between Choice Imitation and Goal Emulation during Human Observational Learning. *Neuron* **106**, 687-699.e7 (2020).
- 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
 (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
 847 Learning. *Neuron* 106, 1044-1054.e4 (2020).
- B48 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
 851 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
 855 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
 857 social decision-making in groups. *Nat. Commun.* 10, 1–12 (2019).
- 40. 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).
- 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).
- 43. 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).
- 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
 869 studies Revisited. *Neuroimage* 84, 971–985 (2013).
- 46. Rigoux, L. et al. Bayesian Model Selection for group studies. Neuroimage 46, 1004–1017 (2009).
- 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).
- Schuck, N. W., Cai, M. B., Wilson, R. C. & Niv, Y. Human Orbitofrontal Cortex Represents a
 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
 880 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).
- 53. Suzuki, S. *et al.* Learning to Simulate Others' Decisions. *Neuron* **74**, 1125–1137 (2012).
- 54. Vickery, T. J., Kleinman, M. R., Chun, M. M. & Lee, D. Opponent identity influences value learning
 in simple games. *J. Neurosci.* 35, 11133–11143 (2015).
- S5. Griessinger, T. & Coricelli, G. The neuroeconomics of strategic interaction. *Curr. Opin. Behav. Sci.* **3**, 73–79 (2015).
- 889 56. Boorman, E. D., O'Doherty, J. P., Adolphs, R. & Rangel, A. The behavioral and neural
 890 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).
- 58. Domenech, P., Rheims, S. & Koechlin, E. Neural mechanisms resolving exploitation-exploration
 dilemmas in the medial prefrontal cortex. *Science (80-.).* 369, (2020).
- 59. Donoso, M., Collins, A. G. E. & Koechlin, E. Foundations of human reasoning in the prefrontal
 cortex. *Science (80-.).* 344, 1481–1486 (2014).
- 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,
 (2019).
- 61. Chung, Y. S., Barch, D. & Strube, M. A meta-analysis of mentalizing impairments in adults with
 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

- 903 computations during strategic interactions in humans. *Proc. Natl. Acad. Sci.* 105, 6741–6746
 904 (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
 908 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