The neuroeconomics of strategic interaction
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We describe here the theoretical, behavioral and neural bases of strategic interaction — multiagent situations where the outcome of one’s choice depends on the actions of others. Predicting others’ actions requires strategic thinking, thus thinking about what the others might think and believe. Game theory provides a canonical model of strategic thinking implicit in the notion of equilibrium and common knowledge of rationality. Behavioral evidence shows departures from equilibrium play and suggests different models of strategic thinking based on bounded rationality. We report neural evidence in support of non-equilibrium models of strategic thinking. These models suggest a cognitive-hierarchy theory of brain and behavior, according to which people use different levels of strategic thinking that are associated with specific neural computations.

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Introduction
Everyday social interactions affect our individual decisions. What makes information relative to others relevant for our own decisional process, and how it is dynamically incorporated in our valuation system remain open questions in neuroscience. The specific case of strategic interactions where the outcome of one’s action depends directly on the other’s behavior narrows down social interactions to situations where each agent should take into consideration not only her own actions, but also the actions of the others [1,2]. Game theory (GT) prescribes precise theoretical solutions for optimal behavior embodied in the premises of rationality (and the notion of equilibrium), and provides a benchmark for the analysis of its behavioral departures. The emergence of bounded rationality models [3–5] and behavioral game theory provide a theoretical framework to unravel the neural roots of strategic reasoning, and shed light on the decision-making mechanisms involved in social interaction. Within this framework, we review work on the neural substrates of equilibrium and nonequilibrium play, and we identify a network associated with strategic thinking in interactive games. In addition, we investigate the interplay between uncertainty and belief inference in repeated interactions with a network related with strategic thinking, thus identifying, respectively, neural substrates of strategic uncertainty and strategic learning.

Theoretical background of strategic interaction
Game theory models strategic interactions as games representing decisions between agents where one’s payoffs depend on the other’s actions, therefore extending the model of individual decision making to the understanding of the interactions in multi-agents situations. Solution concepts provide an answer about which action profile will result from playing a game. Nash equilibrium [6], for instance, prescribes an (optimal) action profile by which no player can increase her payoff by changing her action given the other players’ (optimal) actions. Players are assumed to select strategies that maximize their utility over the payoffs of the game. The choice of the strategies is based on their beliefs about what other players will do. At equilibrium beliefs are correct. Nash equilibrium implies that players’ are certain and accurate about the strategies of the others, indeed the equilibrium is an equilibrium in beliefs that assumes rational expectation and mutual knowledge of beliefs, and thus mutual rationality.

Do people (think and) play at equilibrium?
Equilibrium reasoning (i.e., rationality-based inference) can be cognitively extremely demanding and eventually implausible. Several experimental and empirical studies show behavioral responses that deviate from the prescription of standard game theory, and report extensive evidence of non-equilibrium play [7,8]. From the basic assumptions of strategic reasoning in standard game theory, there are two main departures suggested by behavioral game theory and
Equilibrium and non-equilibrium play in normal form games: an eye-tracking study [15]. The authors used eye-tracking to measure the dynamic patterns of visual information acquisition in two players normal form games (i.e. represented in matrix form). Panel (A) shows the pattern of saccades (i.e. eye movements) performed by 3 typical participants who played as column players (i.e., can take action I or II and have their own payoffs on the top right corner of each cell of the game matrix) in the experiment; (left panel) shows data from a participant who focused her attention on own and other player’s payoffs within each cell of the matrix; (center) focused on own payoffs (i.e., systematically neglected the payoffs of the other player); and (right) players with distributed attention (strategic player). Lines indicate the saccades and the circles the fixation location. Panels (B) and (C) show the first 16 saccades (mean and standard error) in a group of players clustered as distributed attention (strategic players, i.e., level 2 in CH model), divided by equilibrium responses, Panel B: shows that participants started looking at their own payoffs, then they evaluated the payoffs of their counterpart, and finally, they chose their best response when re-evaluating their own payoffs; and out of equilibrium responses, Panel C: showing an undefined temporal pattern of visual analysis. On the right side of each Panel are reported the proportion of own, other and intra-cell saccades at the time of choice (last saccade). These data show how deviation from a distinctive and well-characterized pattern of visual information acquisition determines out of equilibrium behavior.

Adapted from [15].
bounded rationality: the first is about equilibration of beliefs (i.e. the assumption of correct beliefs about the behavior of the others), the second is about errors in the choice process. In what follows we discuss two leading non-equilibrium models of strategic thinking and we report evidence about their neural substrates: (1) Quantal Response Equilibrium (QRE); and (2) level-k and Cognitive Hierarchy (CH) models.3

Non-equilibrium models of strategic thinking

Noisy and stochastic choice: Quantal Response Equilibrium

Quantal Response Equilibrium [9] belongs to a class of bounded rationality models that relaxes the assumption of best response and considers errors in choices, keeping the assumption of (statistically) accurate beliefs and equilibrium responses. In interactive settings, a small amount of noise can have large effect, and QRE models that incorporate stochastic elements in the analysis of interactive decisions can explain ‘anomalous’ behavior (i.e. deviation from rationality) in several experimental games. According to QRE models individuals are more likely to select better than worse actions, but they are often unable to select the very best one. QRE theory has several features in common with findings in recent neuroeconomics literature on noisy and stochastic choice [10]. It has been recently suggested that QRE can be reduced to a form of bounded accumulation models [11,12], a class of models that has been proven relevant to capture under a common theoretical framework stochasticity in value-based decision, reaction time, and visual fixation [13,14]. In a recent paper Polonio et al. [15] observe that equilibrium play in normal form games corresponds to a distinctive and well characterized attentional pattern (in terms of transitions in visual information acquisition between own and other player’s payoffs), and any deviation generates non-equilibrium responses (Figure 1). This suggests how limited attention or noise in the decision process could lead to out of equilibrium behavior.

A cognitive hierarchy theory of brain and behavior

Level-k models [16,17] and Cognitive Hierarchy models (CH, [18,19]) maintain the rational assumption of best
response to beliefs, but relax the assumption of ‘correct’ beliefs (and rational expectation about beliefs). This class of models considers the presence of heterogeneous players in terms of a hierarchy or level of strategic sophistication: level 0 players are strategically naïve (e.g. they play randomly, or do not fully consider the incentives of the game), while higher levels iteratively best respond (i.e. respond optimally) to a distribution (Poisson for CH, and as k-1 for Level-k models) of lower levels players (e.g. L1 best respond to L0, L2 best respond to a distribution of L1 and L0, and so on). Limited strategic thinking (usually 0–2 steps of iteration) is due to limited cognition (limited recursive thinking, limited memory, etc. [20]) and personality characteristics such as overconfidence [21]. According to this model, high-level reasoners (L2 or higher) expect the others to behave strategically, whereas low-level reasoners (L1) choose based on the expectation that others will choose randomly.

Coricelli and Nagel (2009, [22]) ran an fMRI version of the ‘beauty contest game’ — a game suitable for investigating whether and how a player’s mental process incorporates the behavior of the other players in his strategic reasoning [23]. In their fMRI study Coricelli and Nagel found enhanced brain activity in the medial prefrontal cortex (mPFC), rostral anterior cingulate (rACC), superior temporal sulcus (STS) and bilateral tempo-parietal junction (TPJ) when subjects made choices facing human opponents rather than a computer (that chose randomly) in the beauty contest game. This network is often associated to Theory of Mind (ToM) or mentalizing, thus the ability to attribute mental states and beliefs to others [24–27].

Pattern of neural activity related with recursive thinking

When Coricelli and Nagel (2009, [22]) analyzed separately L2 and L1 subjects, they found the activity in the medial prefrontal cortex to be stronger in subjects classified as L2 (Figure 2). Similar result was recently found in Bhatt et al. [28] fMRI results [22] show additional brain activities related to L2 versus L1 reasoning in the lateral orbitofrontal cortex and the dorsolateral prefrontal cortex, areas likely related to performance monitoring and cognitive control [29–31]. This suggests that a complex cognitive process subserves the higher level of strategic reasoning; consistent with the hypothesis that L2 or higher levels imply recursivity (reasoning about reasoning others) and the fact that a strategic player considers the impact of his or her own behavior on the behavior of the others.

Strategic learning

A critical aspect of strategic interactions lies in its time-dependent dynamic. Learning is functional in beliefs formation and in shaping social preferences (i.e. reputation,

![Figure 3](image)

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<tr>
<th>Learning mechanisms</th>
<th>Levels of strategic thinking</th>
<th>Neural correlates</th>
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<tr>
<td>Reinforcement learning (RL)</td>
<td>Level zero k=0</td>
<td>Striatal activity: ( \delta(t) = r(t) - V_0(t) ) RL Prediction error</td>
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<td>Fictitious Play learning (FL)</td>
<td>Low level k=1</td>
<td>rACC</td>
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<td>Influence learning (IL)</td>
<td>High level k=2</td>
<td>mPFC</td>
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<td>( P_{t+1} = P_t + \eta_1 \delta^P_t + \eta_2 \lambda^P_t ) (Hampton et al, 2008)</td>
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Thinking and Learning: computational and neural correlation between strategic thinking and learning. Level zero of strategic thinking can be associated with RL algorithms (Sutton and Barto [49]), low level (level 1) of thinking can be associated with Fictitious play algorithms (Fudenberg and Levine [50]) and high level of thinking (Level 2 or higher) can be associated with Influence learning algorithms. Adapted from [35**–39].
reciprocity etc.). Several studies tackled the dynamic update of belief under a Bayesian framework [32*,33]. Yoshida et al. (2010, [34]) first investigated the neural substrates of (optimal) dynamic beliefs formation in a repeated game in terms of estimates of the opponent's level of strategic sophistication and beliefs uncertainty. The results of this study show that the mPFC plays a role in encoding the uncertainty of inference of the strategy of the (computerized) opponents and the dLPFC is associated with the level of sophistication implemented by the subjects.

An alternative approach, in line with level-k and CH models, has been proposed by Hampton et al. [35**] using learning models incorporating different levels of recursive information integration in repeated strategic games. Interestingly they show that the mPFC, found to support high level of strategic thinking [22], also implements the individual propensity to dynamically incorporate in their learning process a representation of the opponent's adaptive behavior (captured in their model by a parameter of influence, i.e. how one's own actions had influenced the behavior of the other). The role of the mPFC has been found in other studies on social learning [36–38] as representing other's action-reward and action-outcome contingencies. In addition, the implication of the rACC, found to be active for a lower level of strategic thinking [22] has also been shown in repeated strategic games as associated to a lower level of sophisticated learning. Zhu et al. [39] showed for instance that during repeated strategic interactions the activity of the rACC correlates with the estimated departure from reinforcement learning (RL) to (first order) belief leaning. Seo et al. [40] recently showed

**Figure 4**

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<th>(a)</th>
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<th>Gamble</th>
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<th>Gamble</th>
<th>(c)</th>
<th>Sure Payoff</th>
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<th>(d)</th>
<th>Playing entry games: higher level of thinking</th>
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<th>(e)</th>
<th>Strategic Uncertainty</th>
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Strategic Uncertainty: how strategic thinking modulates the perception of risk in games. Participants played lotteries (A), stag hunt games (B), with a sure payoff choice (e.g. 9.50) and an uncertain choice (gamble) in which a player who chooses it gets 15 if at least 4 out of 10 players (including her) choose the gamble and otherwise she gets 0, and entry games (C) with a sure payoff choice and an uncertain choice in which a player who chooses it receives 15 if at most 4 out of all 10 players (including her) choose it and zero otherwise. (D) mPFC activity correlates with choices in the entry games only (thus reflecting higher level of strategic thinking). (E) neural network associated with Strategic Uncertainty (SU, SU entry > SU stag hunt = risk). Adapted from [41**].
that the equivalent area in monkeys encodes the amount of switch from RL, a function of the ability of the computerized opponent to exploit its ongoing learning strategy. All together these results may suggest a cognitive hierarchy of strategic learning mechanisms rooted in a similar level of recursive information integration (see Figure 3).

The role of mPFC in the interplay between deliberation (i.e. degrees of strategic thinking) and strategic uncertainty

Strategic uncertainty arises when the outcome of one’s choice depends on other people’s actions, and thus is the result of strategic interaction. Nagel et al. [41**] investigated how this kind of uncertainty is related to exogenous individual risk and to degrees of strategic thinking (i.e. deliberation). The authors used fMRI to measure the neural correlates of uncertainty in lotteries (i.e. choice under risk) and two kinds of coordination games (i.e. strategic uncertainty), the stag hunt game, where participants have incentives to coordinate on the same action, and the entry game that incentivizes coordination on opposite actions. Solving the former requires low and the latter high degrees of strategic reasoning (of the kind ‘I think that you think that I think etc.’). The results of this study (see Figure 4) demonstrate that a common brain network composed of the thalamus, dorsal medial prefrontal cortex, inferior frontal gyrus and anterior insula (commonly associated to individual risk [42]) is engaged by both individual and social contexts for the resolution of uncertainty. The activity in this network is similar in lotteries and in stag hunt games, but is higher in the entry games. They also found enhanced mPFC activity in the entry games, where more level of strategic thinking is required. Thus, the pattern of activity in the medial prefrontal cortex reflects the interaction between degrees of strategic thinking and uncertainty in interactive games: more deliberation correlates with higher strategic uncertainty.

Conclusions and directions for future work

We can hypothesize that degrees of knowledge of the others and of the context, ranging from certainty to uncertainty, and the different levels of recursive reasoning (depths of reasoning: i.e. the player’s mental processing that incorporates the thinking process of others in strategic reasoning), are crucial factors in the definition of the brain circuits needed to solve strategic interactive situations. The brain data reviewed here provide substantial support for a cognitive hierarchy model of strategic thinking. A higher level is associated with recursive thinking, which is the realization that others can also produce any thought process that we produce, while a lower level reflects self-referential thinking. Different portions of the prefrontal cortex clearly distinguish high-versus-low levels of strategic thinking, and naïve versus sophisticated learning, thus encoding the complexity underlying human social behavior.

We believe that several lines of theoretical research could provide additional relevant insights and tools for the understanding of the neural basis of strategic interaction. Examples are concepts from epistemic game theory (EGT, [43]) and from Global games (GG, [44]). EGT studies the behavioral implications of different notions of rationality and mutual beliefs. EGT can provide important insights into the definition of types of players in terms of beliefs about the structure of the game and the strategies of other players in the game and others’ beliefs, i.e. hierarchies of beliefs. The theory of GG relaxes the assumption of common knowledge and assumes that elements of the game (such as payoffs) are observed with a small amount of noise and that in an ex ante stage of the game any payoff is possible (global games). The assumption is that each player observes a private signal over the course of the payoffs. The result is a unique equilibrium in games with small amounts of noise.

Conflict of interest statement

Nothing declared.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:
- of special interest
- of outstanding interest

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Griessinger and Coricelli


The authors use eye-tracking to classify the participants according to their visual pattern of information acquisition in four classes of two players' normal form games, in which reaching the equilibrium play necessitates to incorporate different levels of information about the other's payoffs. They show individually heterogeneous-but stable-patterns of visual information acquisition based on subjective levels of strategic sophistication and social preferences.


The authors propose that the expected value of a given action in a dynamic coordination game depends directly on subjects' belief over the other's sophistication level. The Bayesian learning model first estimates at each trial the level of strategic thinking of the opponent and then adjusts the subject's level of strategic thinking from which an optimal action is selected.


Using a repeated zero-sum inspection game they show that their influence model fits significantly better than the average choice data of their subjects compared to a simple fictitious play and a reinforcement learning model. The fictitious play first infers from the frequencies of the opponent’s past choices the probability of choosing one action or another, and then decides so as to maximize the action’s consequent expected reward.


The findings of this study suggest a cognitive-hierarchy theory of brain and behavior according to which different levels of strategic thinking are predicted to resolve the uncertainty underlying social interactions.


This article provides a clear and detailed theoretical and conceptual review of the main Non-Equilibrium models in Game Theory along with recent evidence in favor of level-k models.

