

Comparative Game Theory: Bringing Ethology Back into Social Decision Neuroscience



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Abstract Game theory has served as a very useful tool to study complex social behaviors. It provides the mathematical frameworks to formulate various social scenarios to explore behavioral patterns during the interaction. Studies with human subjects have shown that various factors including cognition and social traits influence performance and strategies, and neuroimaging results reveal that multiple brain regions, such as the social brain network and the reward circuits, play crucial roles in strategic interactions. On the other hand, various animal species also show the ability to participate in complex games, with different levels of similarity to human subjects. Animal models allow high-resolution access to neural information at spatial and temporal scales that are currently not possible with human subjects and are thus very suitable for studying the neural basis of strategic social interaction. With advancements in technology and data analysis methods, the field is witnessing

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a surge of exciting new findings that reveal the neural mechanisms under more complex experimental settings. We therefore propose “comparative game theory” as a future direction for the field. We anticipate that by bringing ethology back to social neuroscience studies, we will take full advantage of animal models and understand brain function during strategic social interactions in their most naturalistic form.

1 Introduction

As a social species, our daily lives are characterized by a myriad of interactions aimed at achieving diverse goals. From negotiating with banks for favorable loans to enjoying competitive sports like soccer, wherein teams collaborate to attain victory, social dynamics surround us. To unravel and comprehend these intricate interactions, game theory emerges as a potent tool, employing mathematical frameworks to formulate and analyze social scenarios (Sanfey, 2007; Lee, 2008; Camerer, 2011). Originating from behavioral economics, game theory incorporates concepts such as utilities and payoffs to delineate people’s strategies in various social settings (Camerer, 2011).

While early game theory portrayed individuals as self-interested players solely focused on maximizing personal rewards, it fell short in explaining the complexities of real-life social interactions. Contrary to the notion of humans as self-interested machines, our interactions are deeply rooted in complex cognitive, emotional, and social abilities, constrained by the structures of our brains (Kahneman, 2003, 2011; Kahneman & Tversky, 2012). Consequently, the collaboration between neuroscience, psychology, and economics has emerged in recent years to uncover the neurobiological foundations of social decision-making.

Undoubtedly, complex social dynamics are not exclusive to the human species. Many mammalian and non-mammalian species exhibit intricate social structures, employing diverse strategies in their interactions (Whitehead, 2008). Game theory has also proven instrumental in elucidating these phenomena (Smith, 1982; Trivers, 1985; Weibull, 1997; Dugatkin & Reeve, 2000). In the era of neuroeconomics, animal models have become invaluable tools for studying the neuroscience of complex behaviors (Glimcher & Fehr, 2013). Therefore, combining game theory and ethology provides a unique opportunity to explore the neural mechanisms behind complex social behaviors in diverse interacting scenarios.

This chapter endeavors to spotlight recent advancements deepening our understanding of the neural mechanisms governing complex social interactions. First, we will delve into how game theory serves as an apt framework for neuroscientists and neuroeconomists to explore human social decisions and their neural correlates. Subsequently, we will underscore the significance of using animal models to study the neural underpinnings of complex social decision-making in naturalistic behavioral contexts. Finally, we will conclude by proposing “comparative game theory” as a prospective avenue for the field, advocating for the integration of traditional ethology into neuroscience studies. This holistic approach, facilitated by

technological and computational progress, allows the recording and manipulation of neural activities during naturalistic animal interactions, offering profound insights into the neurobiological and evolutionary foundations of complex social decisions.

2 Game Theory: The Tool to Understand Human Social Behaviors

Rooted in economics, game theory aims to understand the decision strategies in various games. Strategies are the patterns and rules of actions or decisions that subjects employ in response to the environments and partners during the games (Camerer, 2011). To demonstrate the game rules and illustrate the strategies, game theory commonly uses payoff matrices to indicate different action options and the outcomes associated with different action combinations among different players (Fig. 1, example payoff matrices for various games). Payoff matrices are useful tools to demonstrate which actions lead to the best outcomes, and therefore in theory choosing those actions by each player could be interpreted as strategies for playing such games. Game theory was first formally introduced by John von Neumann when he discovered the minimax theorem from the zero-sum games (Camerer, 2011), a family of competitive games in which one player's gain and other players' loss are completely balanced (Fig. 1a). Later efforts had started to focus on the mathematical properties of the payoff matrices. One of the most important discoveries in this regard is the Nash equilibrium. It describes the stability of the strategies applied among players: under certain scenarios, players cannot benefit from changing their current strategy if their partner maintains their current strategy (Camerer, 2011). One of the best examples of the Nash equilibrium is the prisoner's dilemma game (Fig. 1b). In this game, players can either defect or cooperate. Even though cooperation by both players has the highest payoff for both players, the Nash equilibrium is to both defect, because this is the pair of strategies that players from which could not deviate unilaterally because doing so would result in a worse outcome for them. John Nash and other researchers also expanded the application of game theory in broader scenarios such as cooperative games and multiplayer games. Researchers from other fields, such as computer science, political science and biology, also started to apply game theory to their own fields of study. With almost a century of development, game theory has become a very lively and interdisciplinary field today.

Game theory has attained such broad application because the core subject under study—games—is abstract and thus provides a quantitative framework for many scenarios. Real-life social interaction is one of the topics that benefit greatly from game theory. Namely, games themselves are forms of social interaction, and many other types of social interactions can be formulated as games, allowing them to be studied using game theory. Therefore, in recent years, game theory has drawn growing attention from psychologists and neuroscientists who are interested in understanding social behaviors. Early pioneers, such as Reinhard Selten, started to

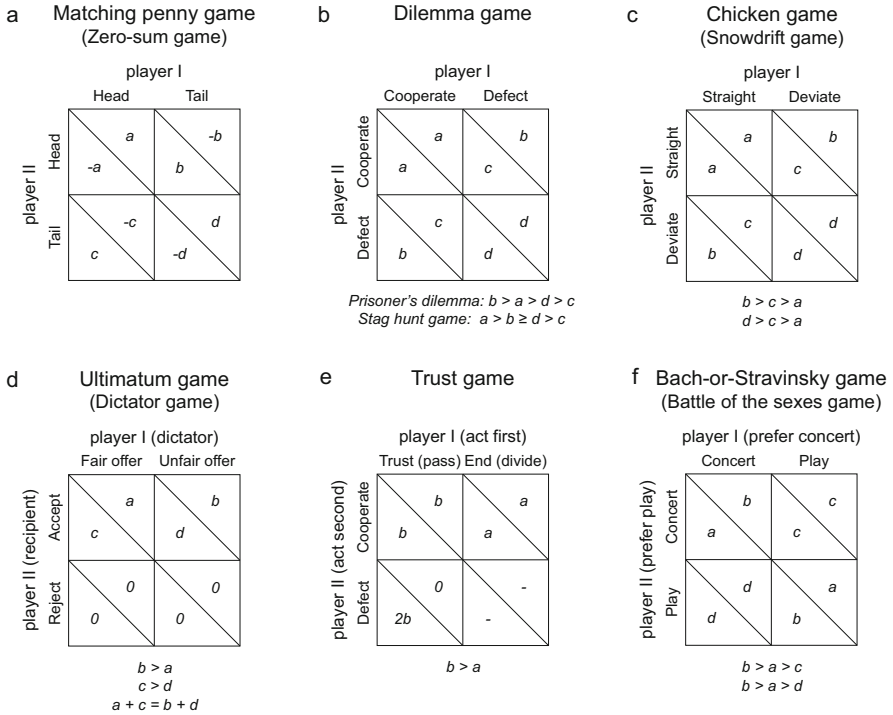


Fig. 1 Payoff matrices for various strategic games. a, b, c, and d indicate the outcome. **(a)** Matching penny game, a type of zero-sum game. **(b)** Dilemma game. If $b > a$, it is a prisoner's dilemma game. "Both defect" is the Nash equilibrium, because of $d > c$. If $a > b$; it is a stag hunt game, which is also referred to as "assurance" game. Stag hunt game has two Nash equilibria—"both stag" because of $a > b$, and "both hare" because of $d > c$. **(c)** Chicken game. It is also referred to as "snowdrift game." The relative values between b and d can vary and will lead to different strategies. **(d)** Ultimatum game. If player II does not have the "reject" option, it becomes a dictator game, which is also referred to as reward allocation game. **(e)** Trust game. If player I chooses to end the game, player II does not need to make a choice (the outcome is indicated as "-" in this case). **(f)** Bach-or-Stravinsky game. It is also referred to as "battle of the sexes" game. The relative values between c and d can vary

design laboratory paradigms and test game theory with experiments on human subjects (Friedman et al., 2004). With the experimental manipulations, researchers were able to examine the predictions of game theoretic models, and more importantly, the experimental game theory has moved the field into a new era of behavioral game theory. The groundbreaking studies done by Daniel Kahneman and Amos Tversky had shown that humans are not rational agents as economists had initially proposed. Human decision-making is limited and influenced by cognitive and psychological processes and thus contains a variety of biases and heuristics (Kahneman, 2003, 2011; Kahneman & Tversky, 2012). Such ideas have also expanded to the social domain and influenced game theory. Specifically, researchers have found that

strategies that people use in the games are influenced by various factors including cognitive biases (Camerer, 2011; Holyoak & Morrison, 2012), emotions (Chang & Smith, 2015), memories (Camerer, 2011; Glimcher & Fehr, 2013), learnings (Fudenberg & Levine, 1998), social preferences (Fehr & Camerer, 2007), and communications (Camerer, 2011). In the era of behavioral game theory, the goal of the field is to understand how these cognitive and psychological factors affect strategic interactions (Camerer, 2011).

Game theory has thus become a major tool to study social behaviors. Psychologists and behavioral neuroscientists have been adapting and developing different versions of games to emphasize and focus on different factors that affect the strategies. For example, to examine the subject's social preference, researchers have designed games with different dilemmas (Fehr & Camerer, 2007). In the dictator game (Fig. 1d), in which one player, the dictator, allocates money between themselves and another player, the recipient, the dictator does not always keep everything, indicating that the player is not purely self-interested and shows prosociality in making those decisions (Güth et al., 1982; Kahneman et al., 1986). The amount of money that the dictator allocates to the recipient also depends on several factors. When the dictator knows the identity of the recipient, they allocate more to the recipient (Eckel & Grossman, 1996; Dana et al., 2006). When comparing the one-shot games with the repeated games, researchers have found that the dictator allocates less to the recipient if they play with the same player multiple times compared with one-shot games (Engel, 2011; Brosig-Koch et al., 2017) and allocate more if the dictator and recipient alternate their roles in the games that encourage reciprocity (Grech & Nax, 2020). If the recipients also have the choice to reject the allocation and eliminate all of the reward, that is, the ultimatum game (Fig. 1d), the dictator tends to allocate more to avoid pure loss (Camerer, 2011; Engel, 2011). On the other hand, if the dictator knows that the recipient is not aware of them being in the game, they will allocate less to the recipient (Dana et al., 2006). These results indicate that in such reward allocation games, players' strategies balance self-interest to maximize their own reward and prosociality to benefit other players. In addition, the fact that the dictator would think about how the recipient understood the game rules and update their strategies accordingly indicates that theory of mind (ToM)—the ability to impute others' mental states (Frith & Frith, 2005)—plays an important role (Yoshida et al., 2008; Harré, 2022). Other example games involving ToM include the prisoner's dilemma game (Fig. 1b) (Press & Dyson, 2012) and the stag hunt game (Fig. 1b) (Yoshida et al., 2008). In these games, the choice of cooperating or defecting strategies depends on the depth of ToM reasoning (Press & Dyson, 2012).

With these fruitful results at hand, the field has started to focus on the neural basis of these strategic social interactions. In the next section, we will highlight the main findings that examined the neural activities of human subjects in various games.

3 Neural Basis of Game Theory

One of the first studies examining neural activity in strategic games was done by McCabe and colleagues (2001). In this study, the participants were playing a trust game (Fig. 1e) with either human or computer counterparts. In this two-player game with sequential actions, player one can first decide to either end the game and divide the reward with player two, or trust player two and pass down the reward. If player one chooses to trust player two, then the overall reward increases, and player two can decide to either divide the reward fairly or take the entire reward. Similar to other dilemma games, the trust game requires player one to have some levels of ToM when making the optimal decision. Functional neuroimaging from these participants showed that for the cooperative players, their neural activities of the prefrontal cortex were enhanced when cooperating with human counterparts, compared with computer counterparts. These results aligned with findings that the prefrontal cortex, especially the medial prefrontal cortex (mPFC), plays an important role in ToM (Frith & Frith, 2006). In addition to mPFC, temporoparietal junction (TPJ) is another brain region that has been found to play a major function in the ToM (Schurz et al., 2014) and during several strategic games (Gallagher et al., 2002; Kircher et al., 2009; Sripada et al., 2009; Speitel et al., 2019).

The social component of game theory is one of the main focuses when exploring its neural mechanism. In addition, under a neuroeconomics framework, game theory is also deeply rooted in reward systems. Therefore, many studies have focused on how the brain's reward circuitry is involved with game theory. Rilling and colleagues found that in a social dilemma game, the activities of the orbitofrontal cortex (OFC) and ventral striatum (VS), the major brain regions of the reward system, were enhanced when the players chose to mutually cooperate (Rilling et al., 2004). Such results implied that reciprocal altruism could be processed as a social reward in the brain, and thus activated the reward circuitry. Altruistic scenarios in other games are also shown to activate the reward system. Mesolimbic–striatal reward system, including the ventral tegmental area (VTA), and OFC were activated when human subjects made altruistic decisions in charity donation tasks (Moll et al., 2006; Harbaugh et al., 2007). In addition, fairness and punishment in the ultimatum games also modulated the neural activity of the reward system (Sanfey et al., 2003; Tabibnia et al., 2008), indicating that emotion, intertwined within the reward system, and cost-benefit calculations (Du & Chang, 2015) also contribute to the neural basis of game theory.

The mesolimbic system, especially the dopamine system, is well appreciated for its crucial role in reinforcement learning (Dayan & Balleine, 2002; Schultz, 2015). Indeed, bridging reinforcement learning with game theory has revealed great insights into the neural basis of strategic social interactions (Nowé et al., 2012). In repeated games, players could learn the payoff matrices and the expected actions of the counterpart via reinforcement learning, in order to choose their own optimal strategies (Nowé et al., 2012). In a repeated trust game (Fig. 1e), King-Casas and colleagues (2005; Tomlin et al., 2006) recorded the BOLD signals of both the

investor (player one) and the trustee (player two) at the same time and found that caudate nucleus of both players encoded an anticipating reciprocal “trust” action of the trustee. They also found that there was a time lag in the peak of encoding between caudate nucleus and cingulate cortex, mirroring the “predictive error” signal found in the reinforcement learning tasks.

In conclusion, brain regions including the social brain network, the reward circuitry, and reinforcement learning system play crucial roles in the neural basis of game theory. Social prediction errors, predictions referenced to other individual’s actions or outcomes, also seem to play a key role (Joiner et al., 2017). However, detailed neural mechanisms are often lacking from experiments done with human subjects due to methodological limitations. It is also challenging to study the causal function of brain regions implicated in strategic games with human subjects. Animal models can give us the access needed to explore neural activity with high resolution and also to probe the causal functions of these neural circuits. In the following sections, we will discuss the possibility of using animal models to study game theory, especially its neural basis, and highlight the benefits of using animal models.

4 Can Animals Play Strategic Games?

The application of game theory is not limited to explaining human behaviors. Other animals also have complicated interactions between individuals of the same species and across different species. Combined with evolution theory, John Maynard Smith and others proposed “evolutionary game theory” to understand animals’ natural social interactions and decisions, such as cooperation, altruism, and competition, through the lens of natural selection (Smith, 1982; Weibull, 1997). It emphasizes how strategies evolved over time based on their success or fitness within a given environment. For example, the adapted models from game theory have been shown to explain the predator-prey interaction (Brown et al., 1999), mating behaviors (Roughgarden et al., 2006), as well as kin selection in altruistic behaviors (Ohtsuki, 2010). These fruitful results demonstrate that animals show complex strategic interactions ethologically and ecologically.

Such results provide the foundation to explore different species’ capability in strategic social interactions and decisions. A large effort has been put into studying these questions in various experimental settings over the past several decades. Different species of nonhuman primates have been shown to participate in various strategic games. Chimpanzees (*Pan troglodytes*) have been shown to strategize when playing the ultimatum game (Fig. 1d) (Proctor et al., 2013), reward allocation games (Fig. 1d) (Melis et al., 2009), stag hunt games (Fig. 1b) (Bullinger et al., 2011), and competition games (Knofe et al., 2019). Other nonhuman primates also employed different strategies in complex social games, including bonobos (*Pan paniscus*) (Sánchez-Amaro et al., 2017; Sánchez-Amaro & Rossano, 2021), macaque species (*Macaca mulatta*; *Macaca fuscata*; *Macaca fascicularis*) (Reinhart et al., 2010; Brosnan et al., 2011, 2012; Kaigaishi et al., 2019; Sigmundson et al., 2021),

capuchins (*Sapajus apella*) (Brosnan et al., 2006; Addessi et al., 2011; Smith et al., 2019), and common marmosets (*Callithrix jacchus*) (Burkart et al., 2007; Burkart & van Schaik, 2020; Martin et al., 2021; Sánchez-Amaro et al., 2021). In addition to nonhuman primates, many other animals are also able to strategize when interacting with conspecifics. For example, elephants (*Elephas maximus*) (Plotnik et al., 2011), wolves (*Canis lupus*) and dogs (*Canis familiaris*) (Marshall-Pescini et al., 2017), and different kinds of birds (Schwing et al., 2016; Heaney et al., 2017; Torres Ortiz et al., 2020) employ cooperative strategies in cooperation games, and wolves and dogs are able to coordinate to solve the social dilemma in coordination games (Bräuer et al., 2020).

While there is no doubt that many animals have the ability to strategize in sophisticated social interactions, it is particularly interesting and important to compare similar or dissimilar strategies across nonhuman species and with humans. In some cases, different species adapt very similar strategies. For example, capuchin monkeys, chimpanzees, and humans have been found to use very similar strategies in the stag hunt game (Fig. 1b) (Brosnan et al., 2011). On the other hand, different species can also adapt different strategies even when they are playing the same game, such as chimpanzees and human children in the same stag hunt games (Duguid et al., 2014). The difference in strategies employed by different species might be the result of their varying levels of prosociality inherent to the species' ethology. In a modified dictator game (Fig. 1d) designed for nonhuman primates (group service game) such that one animal has to pull a board to altruistically provide food to another animal, Burkart and colleagues compared performances among marmosets, capuchin monkeys, and macaques (Burkart & van Schaik, 2013). They found that marmosets had the highest and most stable pulling rates during the game, capuchin monkeys had the intermediate level, and macaques made no altruistic pullings. Importantly, these behavioral results are consistent with the breeding patterns of these species in the wild: marmosets breed cooperatively, macaques breed independently, and capuchin monkeys have an intermediate breeding system, indicating that their performance in the task could be a reflection of their natural prosociality, with marmoset having the highest prosociality and social tolerance (Burkart & van Schaik, 2013; Burkart & Finkenwirth, 2015).

Even within the same species, the prosocial traits of individuals also affect their strategies (Weinberg-Wolf & Chang, 2019). More prosocial marmoset individuals tend to offer more altruistic actions in the group service game and make more cooperative choices (Martin et al., 2021). Japanese macaques with higher social tolerance levels also performed better in the cooperative tasks compared with conspecifics with lower social tolerance (Kaigaishi et al., 2019). In fact, a wide range of social factors can influence prosocial traits and lead to different strategies. In a task where marmosets sat across from each other with a single lever between them, males and females demonstrated distinct strategies. In the competition condition, where the first marmoset to pull the lever received a larger reward, females tended to pull the lever faster (Sánchez-Amaro et al., 2021). However, in the snowdrift condition, where the first marmoset to pull received a smaller reward, females tended to wait longer before pulling, suggesting they were waiting for their partner

to pull. In contrast, male marmosets did not differentiate between the two conditions, pulling the lever after the same amount of time in both scenarios (Sánchez-Amaro et al., 2021). Importantly, the different strategies played by different sexes are consistent with the food sharing behaviors of marmosets in the wild, where female breeders show the lowest levels of food sharing likely due to their energetic demands for reproducing (Guerreiro Martins et al., 2019). Dominance rank may also affect individuals' prosociality. For example, dominant macaques made more altruistic choices in a dictator game than the subordinate conspecifics (Massen et al., 2010; Chang et al., 2011).

Cognitive capacity may also lead different species to adopt different strategies (Melis & Raihani, 2023). Wang and Kwan compared the performance of macaques (Seo et al., 2009) and mice (Wang et al., 2022) playing matching penny games (Fig. 1a) (Wang & Kwan, 2023). They found that even though both species played against the computer with the identical algorithm, mice tended to adopt simpler strategies such as win-stay-lose-shift and had stronger choice biases, while macaques adopted their strategies based on the interactive outcome with their opponents. One might argue that the biggest challenge of cross-species comparisons is deciphering if behavioral differences are due to different training processes, instead of due to varied social or cognitive capabilities of different species. Researchers therefore need to carefully consider these alternatives.

Some studies have shown great insights into this challenging aspect of comparative game theory. Brosnan and colleagues carefully controlled the training procedures for capuchin monkeys, chimpanzees, and human subjects and found that with identical training, these species had very similar performance in the stag hunt game. Especially, when human subjects played the nonhuman primate friendly version, their performance was more similar to the nonhuman primates compared to typical human performance (Brosnan et al., 2011). In a more recent study, Moeller and colleagues compared humans' and macaques' performance in a coordination game "Bach-or-Stravinsky" (Fig. 1f, battle of the sexes game) in the same transparent touchscreen settings (Moeller et al., 2023). In this game, two players had opposite preferences for choosing one action over the other, and the optimal strategy was to dynamically take turns for each option to equalize the payoffs. Human dyads developed such coordinated behaviors, while macaque dyads converged to a simple and static strategy entailing strong biases. Interestingly, when paired and trained with human counterparts, macaques were able to learn and adopt the dynamic turn-taking strategy. In rodent models, researchers also showed that with careful control of the training process and the animal's motivation level, rats were able to use complex strategies in an iterated prisoner's dilemma game, similar to human subjects (Viana et al., 2010). Altogether, these investigations emphasize the importance of experimental and task designs in cross-species work. They showed the possibility that even with different prosocial and cognitive capacities from humans, animal subjects can develop and adopt human-like strategies in complex games with carefully considered training procedures.

Overall, across different species, some animals show similar strategies as humans, while some don't. The differences and similarities depend on the cognitive

ability of different species, as well as their social traits. Comparing the strategies across species can help us understand our own social behaviors from an evolutionary perspective and also provide us with a chance to use animal models to study the neural basis of strategic social interactions in much greater detail. The next section will discuss some of the major findings on this aspect.

5 The Benefit of Animal Models in Game Theory

The biggest benefit of working with animal models is that they give us much more access to direct neural information at high spatial and temporal resolution that is very challenging or impossible to obtain from human subjects. Specifically, as discussed in the previous section, many species could display similar performance as human beings in various strategic games. As long as the context of the games is largely compatible with the animals' ethology, such similar performances can be leveraged to reveal the neural basis behind these strategic interactions that could translate to the human brain.

Over the years, macaque monkeys have been the most prevalent animal model to study the neural basis of decision strategies (Lee, 2008). In a modified dictator game involving pairs of macaques, an actor monkey had choices to allocate the reward to themselves, the partner monkey or neither of them (Fig. 2a). While the animals were performing the task, Chang and colleagues recorded the neural activities from the dictator animals' ACC and OFC (Chang et al., 2013). The results showed that the majority of OFC neurons encode the reward that was received by the "dictator" monkeys themselves. On the other hand, they found that many neurons in the ACC gyrus encode the reward outcome of the recipient, either exclusively or similarly to the reward received by the dictator. Finally, the majority of neurons in the ACC sulcus were found to encode the foregone reward (rewards that the dictator did not receive). These results indicated that neurons from different prefrontal cortical areas represent reward outcomes from the dictator game using different frames of reference—some neurons use self-centered frames of reference, whereas other neurons use either partner-centered or both-centered frames of reference. OFC and ACC sulcus were shown to be biased toward using a self-centered frame of reference, whereas ACC gyrus had a bias toward signaling the partner's reward outcome (i.e., partner- or both-centered). A subsequent study by the same team found that neurons in the BLA exhibited correlated value tuning between the reward of the dictator and the reward of the partner (Chang et al., 2015), indicating the role of BLA in shared value coding between self and other in social decision-making. When the researchers recorded the activity of ACC gyrus and BLA simultaneously during the same dictator game, they found that making prosocial choices or antisocial choices enhanced frequency-specific and direction-selective coordination of activity between BLA and ACC gyrus (Dal Monte et al., 2020), suggesting that specialized communication in the prefrontal-amygdala networks may guide social decision-making (Fig. 2a).

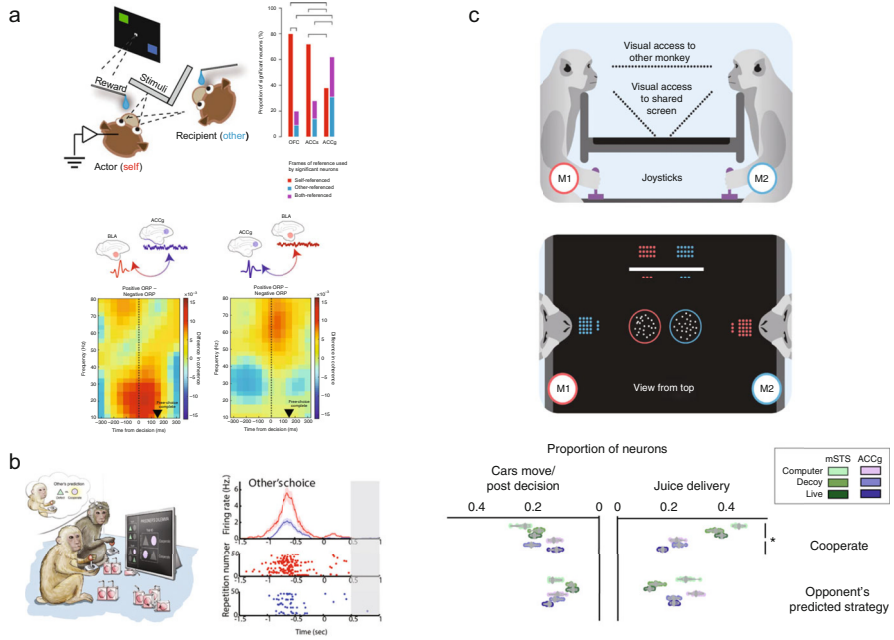


Fig. 2 Example studies that examine the neural mechanism while macaque monkeys participate in various games. **(a)** Macaques in a dictator game (Chang et al., 2013; Dal Monte et al., 2020). Top left panel demonstrates the experimental setup, in which animals are head fixed. Actor macaque decides to allocate the juice to self, other, both, or either. Top right panel summarizes the encoding properties of OFC, ACCs, and ACCg, with OFC and ACCs bias toward self-centered frame of reference and ACCg bias toward other-centered frame of reference. Bottom panel shows the frequency-specific and direction-selective coordination of activity between BLA and ACCg for the prosocial and antisocial choices, respectively. **(b)** Macaques in a prisoner’s dilemma game (Haroush & Williams, 2015). Left panel demonstrates the experimental setup, in which animals are head fixed, but with free hand movement. Right panel highlights one example ACC neuron that predicts partners’ choice to either cooperate (red) or defect (blue) that is yet unknown to the recorded animal. **(c)** Macaques in a chicken game (Ong et al., 2021). Top and middle panels show the experimental setup, in which animals are head fixed, but with free hand movement and free viewing of partner and shared screen. Bottom panel summarizes the percentage of neurons in mSTS and ACCg that encode animals’ own strategies (cooperate or not) and partners’ predicted strategies. Example studies like the one in (c) allow researchers to explore larger behavioral repertoires. (Panels (a) to (c) are adapted from published literature with permission)

ACC has also been investigated when pairs of macaques played an iterative version of the prisoner’s dilemma game (Fig. 2b) (Haroush & Williams, 2015). In this study, researchers found that the activity of ACC neurons predicted partners’ choice to either cooperate or defect that was yet unknown to the recorded animal. Further analysis revealed that ACC neurons kept track of the outcomes from the previous interactions in order to predict future choices (e.g., the likelihood of mutual cooperation was higher following mutual cooperation from the previous round), and disrupting the ACC activity led animals to make less mutually beneficial choices,

likely due to a disruption in predicting partner's choices. Moreover, in a three-agent reward allocation game, researchers found that the dmPFC/ACC neurons tracked the previous interactions among individuals within the group and integrated this information with animals' identities to guide the subject's choice of reciprocating or retaliating (Báez-Mendoza et al., 2021). Notably, microstimulation applied to these neurons led animals to make less mutually beneficial choices. These results raise the possibility that ACC and dmPFC are key regions underlying social prediction and inference, an important component of the theory of mind (ToM).

In the human brain, the temporal-parietal junction (TPJ) and the mPFC play central roles in the theory of mind. Interestingly, while nonhuman primates do not have anatomically defined TPJ, the middle superior temporal sulcus (mSTS) was found to be a homologous area to the human TPJ based on comparative functional connectivity (Mars et al., 2013). Recently, researchers have examined the role of the mSTS and mPFC in the chicken game (Fig. 1c, a type of snowdrift game) played by macaques, in which two monkeys faced each other and controlled the moving direction of their virtual cars (Fig. 2c) (Ong et al., 2021). In this game, going straight without crashing yields a large reward, but deviating yields a small "chicken" reward. However, both animals going straight causes a crash of their card, no rewards for both animals. Behaviorally, monkeys developed a complex strategy that was more sophisticated than simple "tit-for-tat" or "win-stay-lose-shift" strategies by actively using and updating the payoffs for both themselves and the partners while taking into account the partners' predicted actions to guide their own actions. At the neural level, researchers found that mSTS carried key information about cooperative strategies.

Taken together, these studies in monkeys demonstrate the advantages of animal models in combining game theory with neuroscientific inquiries. Consistent with the human research, these studies also found the critical functions of OFC, mPFC areas such as ACC and dmPFC, mSTS, and BLA in strategic social interactions (Gangopadhyay et al., 2020). More importantly, several studies identified the specified and causal function of these brain regions and how the communication across these brain regions is involved in social decisions.

Recent efforts have also explored a larger variety of animal models. Jiang and colleagues recorded the OFC activity while rats were participating in a cooperative interaction, in which two rats need to poke their noses at the nose ports at the same time to receive a reward (Fig. 3a) (Jiang et al., 2021). They found that OFC neurons encoded various variables related to the strategies, including the payoffs, the outcomes, as well as the roles (initiator or follower) of the subjects and their partners. Such findings were consistent with the function of OFC in human studies (Rilling et al., 2002, 2004). Although rodents may not be capable of quite as complex strategies as humans and nonhuman primates, studying the neural mechanisms underlying social game processes in rodents can help us better understand more detailed physiological processes underlying mammalian social and interactive behaviors. The advantage of rodent models is the genetic tools they provide to study the neural mechanisms at cellular and subcellular levels, including the functions of different cell types and neuromodulators. Although these

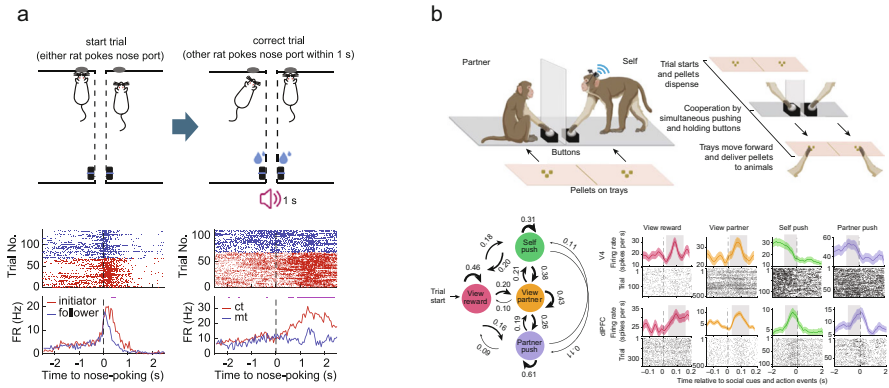


Fig. 3 Example studies that examine the neural mechanism in cooperative games with various animal species in freely moving conditions. **(a)** Rodents in a strategic cooperative interaction (Jiang et al., 2021). Top panel shows the experimental setup, in which animals are freely moving. Two rats are required to cooperatively poke their noses at the ports within 1 s to receive juice reward. Bottom panels show two example OFC neurons that encode the roles of the recorded animal (poke initiator or follower) and the trial types (ct: cooperative trial, or mt: missed trial). **(b)** Macaques in a strategic cooperative interaction (Franch et al., 2024). Top panel shows the experimental setup, in which animals are freely moving and neural activity is recorded with a wireless recording system. Bottom left panel shows the viewing and pushing behaviors and the transitions between behavioral epochs. Bottom right panel highlights example neurons from V4 and dlPFC and their activity aligned with different behavioral events. Compared with studies in Fig. 2, these experimental setups become more naturalistic, with no restraints on animals’ actions. These two studies also highlight that animals across different species are able to do similar strategic interaction tasks. (Panels (a) and (b) are adapted from published literature with permission)

approaches have been underutilized in strategic social decision-making, in a recent study researchers found that the noradrenergic and cholinergic activity of the mouse frontal cortex encoded the key decision variables and played a causal role in the strategies when the animals were engaging in a matching penny game (Wang et al., 2024). Altogether, these results paved the way for future research to fully explore the opportunities of using rodent models to study the neural basis of game theory.

6 Future Direction: Game Theory in the Wild

In this chapter, we summarized the main concepts of game theory and the literature that examines the neural mechanisms behind strategic social interactions. We specifically reviewed that various animal species are capable of participating in strategic games, and their performances can be compared with those of human subjects. We also discussed and emphasized the advantage of introducing animal models when exploring the neural basis of social strategy. However, it is essential to carefully consider the key differences between animal models and humans—such as

genetic backgrounds, brain anatomies, social structures, and cognitive capabilities—when interpreting results from animal studies and drawing insights for human applications (Hartung, 2008; Al Dahhan et al., 2019).

In addition, there remains a major challenge that is yet underexplored. In traditional settings, neuroscience research usually restrains the subjects' movements—human subjects are required to minimize their movements in the MRI machine, and animal subjects are head-restrained in order to record stable neural activity with either electrodes or microscopes, or monitor eye positions. In real-life social interactions, however, humans and nonhuman animals show a much richer behavioral repertoire. Limiting access to naturalistic behaviors will limit the type of social information that subjects can receive and send. For example, gaze is an important social cue for humans and nonhuman primates in social interaction. Gaze patterns have been found to influence people's strategies in cooperation and competition games (Jarick & Kingstone, 2015). People also strategize gaze behaviors to convey information to others in various games (Hausfeld et al., 2021). Nonhuman primates also show complex gaze patterns in naturalistic social interactions (Dal Monte et al., 2016, 2022; Fan et al., 2023) and actively use gaze to collect information while engaging in cooperation tasks (Fig. 3b) (Franch et al., 2024), “chicken” game (Fig. 2c) (Ong et al., 2021) and “Bach-or-Stravinsky” game (Moeller et al., 2023). In the “Bach-or-Stravinsky” game, if the subjects' view of the opponents was blocked, their strategies were changed and became less optimal (Moeller et al., 2023). In addition, the neural encodings between restrained and naturalistic conditions also appear to be different. For example, researchers found that PFC neurons in marmosets represented the same social information differently across head-restrained, freely moving, and communicational conditions, and the neural tunings can flexibly adapt to the dynamics of each condition (Jovanovic et al., 2022). Altogether, these results emphasized an important future direction for the field—to study the neural basis of game theory in its naturalistic form. Indeed, strategically balancing experimental control and ecological validity is increasingly becoming an important issue in social neuroscience research (Fan et al., 2021).

One way to explore this direction is to design experimental apparatus with more naturalistic settings (Fan et al., 2021; Miller et al., 2022). For human studies, researchers have begun to use more portable equipment to record neural activity while participating in games, such as functional near-infrared spectroscopy (fNIRS) (Zhang et al., 2023) and wearable electroencephalography (EEG) (Hafeez et al., 2021). Various wireless recording systems have been developed for rodents (Kim et al., 2020; Yang et al., 2022), bats (Zhang & Yartsev, 2019; Rose et al., 2021), marmosets (Roy & Wang, 2012; Walker et al., 2021; Jendritza et al., 2023; Meisner et al., 2024), and macaques (Schwarz et al., 2014; Franch et al., 2024; Shahidi et al., 2024; Testard et al., 2024) that allow researchers to explore the neural mechanisms when animals can move freely and behave more naturally than before (see Fig. 3b, an example study that recorded neural activities while macaques were performing a cooperative task in a freely moving manner).

Overall, a promising and important future direction for the field is to bring ethology back to the social decision neuroscience. The experimental designs could

be naturalistic; however, they still require certain aspects of the social interactions to be abstracted and symbolized. Humans use game theory not only to strategize poker games but also in daily life, such as bargaining for goods. Animals never press buttons or pull levers in the wild; however, they can use complex strategies to forage food or claim territory in group settings. With the recent development of techniques to precisely and markerlessly track naturalistic behaviors of multiple individuals and to perform wireless neural recording, we are now witnessing a surge in computational neuroethology (Anderson & Perona, 2014; Datta et al., 2019; Mobbs et al., 2021; Cisek & Green, 2024). We anticipate that the study of strategic social interaction will follow this trend, and in the near future, we will see more exciting results revealing the neural mechanisms of our complex social behaviors in their naturalistic forms.

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