



Competitive and cooperative games for probing the neural basis of social decision-making in animals

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ABSTRACT

In a social environment, it is essential for animals to consider the behavior of others when making decisions. To quantitatively assess such social decisions, games offer unique advantages. Games may have competitive and cooperative components, modeling situations with antagonistic and shared objectives between players. Games can be analyzed by mathematical frameworks, including game theory and reinforcement learning, such that an animal's choice behavior can be compared against the optimal strategy. However, so far games have been underappreciated in neuroscience research, particularly for rodent studies. In this review, we survey the varieties of competitive and cooperative games that have been tested, contrasting strategies employed by non-human primates and birds with rodents. We provide examples of how games can be used to uncover neural mechanisms and explore species-specific behavioral differences. We assess critically the limitations of current paradigms and propose improvements. Together, the synthesis of current literature highlights the advantages of using games to probe the neural basis of social decisions for neuroscience studies.

1. Introduction

Many animal species are social and interact frequently with conspecifics. When making decisions, the animals must consider not only the physical consequences of their actions, but also the behavior of others. Research has shown that decision-making in a social context recruits unique neural circuits and brain regions (Apps et al., 2016; Báez-Mendoza et al., 2021; Chen and Hong, 2018; Fareri et al., 2012; Gangopadhyay et al., 2021; Lee and Seo, 2016; Padilla-Coreano et al., 2022; Zhou et al., 2018). However, in most settings, social decisions are unconstrained such that animals can engage each other in countless number of ways, which presents challenges for quantification and interpretation of the neural correlates. One approach to study social decisions in a controlled environment is to have animals play games (Lee, 2008).

Games can be studied within the formalism of game theory. Potential actions and their corresponding outcomes are captured by a lookup table known as the payoff matrix. Interactions involving multiple individuals are analyzed mathematically to understand the optimal strategies

(Osborne, 2004). As a testament to their versatility, games have been used as models to investigate real-life economic, political, and biological decisions when aligned and competing interests are involved (Durlauf and Blume, 2010; Konyukhovskiy and Holodkova, 2017). Artificial intelligence has been developed to play games proficiently (Bakhtin et al., 2022; Brown and Sandholm, 2018; Moravčík et al., 2017), providing insights into the latent learning process. Moreover, different species can be trained to play the same game, facilitating comparisons across animals to highlight similarities and differences in their neural implementations for social decision-making.

In this article, we start by giving a brief background of game theory. We will then elaborate on studies of animals engaging in various kinds of competitive and cooperative games. We will summarize the current knowledge regarding neural mechanisms of strategic game play. We will conclude by discussing the limitations in current experimental designs and opportunities for future studies.

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2. The basic components of a game

A game models a decision-making problem involving a set of individuals referred to as agents or players. Games may be played sequentially, when a player can observe the opponent's decision before making its own, or simultaneously, when the players decide at the same time without such knowledge. Actions can be performed via different kinds of operandum to suit the species playing the game. For example, actions can be indicated by directional eye movements for nonhuman primates and directional tongue licks for rodents. Juice drops and food pellets may be used as rewarding outcomes for macaques and rats respectively. In some studies involving macaques, outcome is tabulated by abstract tokens (e.g., 6 virtual tokens shown on a computer monitor to exchange for a juice drop), which is particularly appealing because both gains and losses can be tracked (Seo et al., 2014). Games are challenging because of imperfect information: a player does not have full knowledge of the other player's action and/or strategy.

The payoff matrix or extensive form describes all the possible actions that players can take and the corresponding outcomes. Based on the payoff matrix, the strategies and their expected payoffs can be analyzed quantitatively. A strategy refers to a set of probabilities linked to the available actions at a given stage of the game, guiding the animal's behavior. Specifically, a pure strategy refers to a deterministic policy of choosing one specific action, whereas a mixed strategy defines a policy with non-zero probabilities of choosing among two or more pure strategies. Assuming players act rationally to maximize their own payoff, optimal strategies called Nash equilibria for all players involved in the game can be calculated.

Games can be competitive or cooperative. Some of the most common competitive and cooperatives game, as well as their payoff matrices are shown in Fig. 1. In competitive games, one player's gain is tied to another player's loss, resulting in opposite incentives. In cooperative games, players may choose to join forces to obtain a smaller but safer reward, by forgoing the best payoff but also a risk of a greater loss

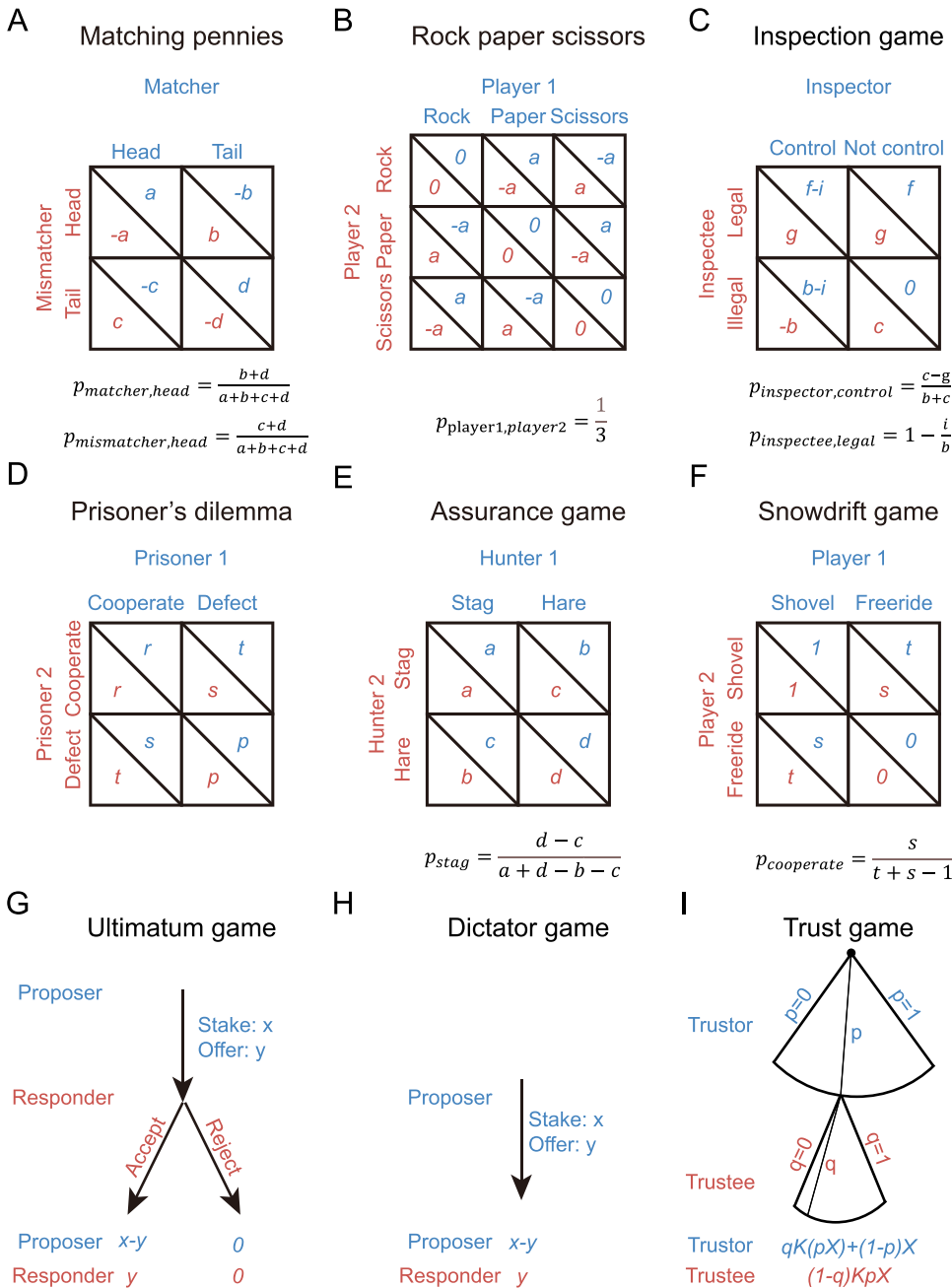


Fig. 1. Social games used in animal decision-making. (A) Payoff matrix for matching pennies. a, b, c, d denote the amount of outcome gained or lost depending on the actions. (B) Payoff matrix for rock-paper-scissors. a denotes the amount of outcome. Blue and red text indicating the actions and outcomes for the corresponding players. (C) Payoff matrix for inspection game. i denotes the cost of inspection. $c > g$. (D) Payoff matrix for prisoner's dilemma. $t > r > p > s$. (E) Payoff matrix for assurance game. $a > b > d > c$. (F) Payoff matrix for snowdrift game. $t > 1 > s > 0$. (G) Extensive form representation for ultimatum game. The proposer offers the responder y , while the total outcome is x . If the responder accepts, the proposer gets $x-y$, the responder gets y . If the responder rejects, both players get 0 . (H) Extensive form representation for the dictator game. The proposer offers the responder y out of x , which is the final decision. (I) Extensive form representation for trust game. The trustor gives a proportion (p) of the reward X , which is multiplied by K when the trustee gets it. Then the trustee gives another proportion (q) back to the trustor. Both p and q can be 0 .

individually. Playing close to the Nash equilibrium is usually the best strategy, because the animal can maximize rewards and be unbeatable in competitive games, even if the opponent is aware of the strategy. The Nash equilibrium may be deduced through reasoning of the payoff matrix, which is possible for humans playing simple games, though it is usually learned through extensive play, as exemplified by computer players (Brown and Sandholm, 2018). In practice, behavior may deviate from the optimal strategy as prescribed by the Nash equilibrium due to the use of heuristics (simple decision rules; e.g., win-stay lose-switch), biases (preference towards certain action; e.g., choosing left more due to innate inclination unrelated to reinforcement), or limited cognitive abilities (e.g., finite depth of reasoning) (Camerer, 2011; Shettleworth, 2009). Therefore, game theory provides a quantitative framework to describe rational decision-making and find deviations from the predictions.

While the behavioral apparatus can be customized to use actions and outcomes that suit an animal, it is more difficult to ascertain that the species in question possesses the cognitive abilities to comprehend the action-outcome contingencies and enact sensible strategies. Most animal studies of games to date have used one of three models: non-human primates, rodents, and birds. Non-human primates are known for their advanced cognitive and social abilities (Strier, 2016), which makes them the most widely studied animal models for games. Apes, such as chimpanzees, and monkeys, such as macaques, capuchins, and squirrel monkeys, are among species studied. Rodents can form complex social structures in the wild (Lacey et al., 2007) and engage conspecifics in reciprocity (Bartal et al., 2011), territorial aggression (Thurmond, 1975; Weber et al., 2017) and formation of social hierarchies (Fan et al., 2019; Williamson et al., 2016). An obvious strength for rodent models is the availability of powerful genetic tools for neural circuit dissection (Luo et al., 2018). In addition to mammals, many birds are highly social. Avian societies are dynamic in terms of group membership, which constitutes mostly non-breeders (Boucherie et al., 2019; Silk et al., 2014). Birds exhibit social traits including cooperation and reciprocity (Ligon, 1983). Considering the distinct brain structures in avian and mammalian species (Cobb, 1960; Jarvis et al., 2005), similarities in social behavior may arise from convergent evolution. That said, there have been fewer studies with birds engaging in social games relative to mammals. The study of the same games using different animal models may reveal distinct neural circuits developed to implement similar behavioral algorithms.

3. Competitive games

Many instances of competition between animals have been identified, such as when they fight for resources like food and parental attention (Hudson and Trillmich, 2007; O'Connor, 1978), mating right (Clutton-Brock, 2017), and territory (Hinsch and Komdeur, 2017). Competitive games, which come in several flavors, are aimed at modeling such adversarial situations.

3.1. Matching pennies

A classic competitive, zero-sum game is matching pennies, where two players choose simultaneously to either show the head or tail side of their coin. If the sides match (e.g., head and head), the “matcher” player gets a reward from the other “mismatcher” player (Fig. 1A). By contrast, if the sides are different (e.g., head and tail), the mismatcher wins at the expense of the matcher. The Nash equilibrium specifies the probability for each player to choose head versus tail to maximize payoff:

$$p_{\text{matcher,head}} = \frac{b+d}{a+b+c+d};$$

$$p_{\text{mismatcher,head}} = \frac{c+d}{a+b+c+d}$$
(1)

In the special case of a symmetric game ($a=d$, $b=c$), the Nash

equilibrium states that both players should pick the sides randomly with equal probabilities and expect to win 50% of the trials in the long run. When the payoff matrix is asymmetric, players may be pressured to bias towards one action.

Various species have been trained to play the iterated form of matching pennies for many trials in a single session. Against a computer opponent, macaques (*Macaca mulatta*) can adjust their strategy when confronted with growing pressure placed by a savvy competitor (Barclough et al., 2004; Lee et al., 2004; Thevarajah et al., 2009; Thevarajah et al., 2010). Specifically, if the computer was indifferent of the monkey's decisions, the macaque's strategy strongly depended on its history of past choices and outcomes. When the computer switched to a more competitive algorithm to take advantage of systematic deviations from the Nash equilibrium, the macaque adapted to become more unpredictable. In an asymmetric matching pennies game, macaques performed well although did not operate exactly at the optimal solution, instead choosing the biased action less frequently than a rational agent (Seo et al., 2014).

Chimpanzees (*Pan troglodytes*) can play games with each other via touch-panel screens. In both symmetric and asymmetric matching pennies, they can find the Nash equilibrium and employ the optimal strategy (Martin et al., 2014). Interestingly, the chimpanzee playing the matcher responded faster than the mismatcher, consistent with tendencies exhibited by human players (Attali and Bar-Hillel, 2003; Eliaz and Rubinstein, 2011). The different response times may stem from specialized neural circuits dedicated to mimicking and following the other's action. Furthermore, chimpanzees achieved high reward rates, often surpassing those of humans. This could be attributed to their higher working memory capacity (Matsuzawa, 2009) or their familiarity with social dominance and competitive situations (Boehm and Boehm, 2009; Martin et al., 2014).

In addition to the non-human primates, rats can adjust their behavior when playing against computers with escalating competitive pressure (Skelin et al., 2014; Tervo et al., 2014). Rats accrued comparable reward rates playing against successively stronger opponents, suggesting that they quickly switched to more stochastic behavior when facing growing pressure. Pigeons (*Columba livia*) were trained to play both symmetric and asymmetric matching pennies with a conspecific (Sanabria and Thrailkill, 2009). The birds played the games efficiently, exhibiting different choice behaviors in accordance with the variations in the payoff matrices. Collectively, these studies show that several animal species can effectively play matching pennies against computers or conspecifics, at a performance approaching the Nash equilibrium.

An exciting direction is to contrast game performance across species. As one example, we compared the performance of macaques (Lee et al., 2004; Seo et al., 2009) and mice (Wang et al., 2022) playing matching pennies. Although macaques and mice (*Mus musculus*) were trained with different apparatuses, they were playing the same game and faced a computer opponent programmed with the identical strategy (Fig. 2A). Their choice behaviors were analyzed by fits of computational models based on reinforcement learning. Reinforcement learning provides a normative description of the behavior, and facilitates quantitative comparisons (Liao and Kwan, 2021). The comparison revealed that choice behaviors in matching pennies for macaques and mice broadly resembled each other, however there were also differences (Fig. 2B, C). (Lee et al., 2004; Wang et al., 2022). The probability of adopting win-stay-lose-switch for macaques was positively correlated with the learning rate of the model, yet there was no correlation for mice (Fig. 2D). This difference suggested that the macaques rely more on feedback from outcomes, while mice are biased toward previous choices. Logistic regression analyses indicated that choice behavior of both macaques and mice depended on the interaction of previous choices and outcomes, referred to as the reinforcer effect (Fig. 2E, F). Mice were biased more strongly by the last reinforcer, whereas macaques considered several trials into the past. These results illustrate that primates and rodents may employ comparable learning algorithms to

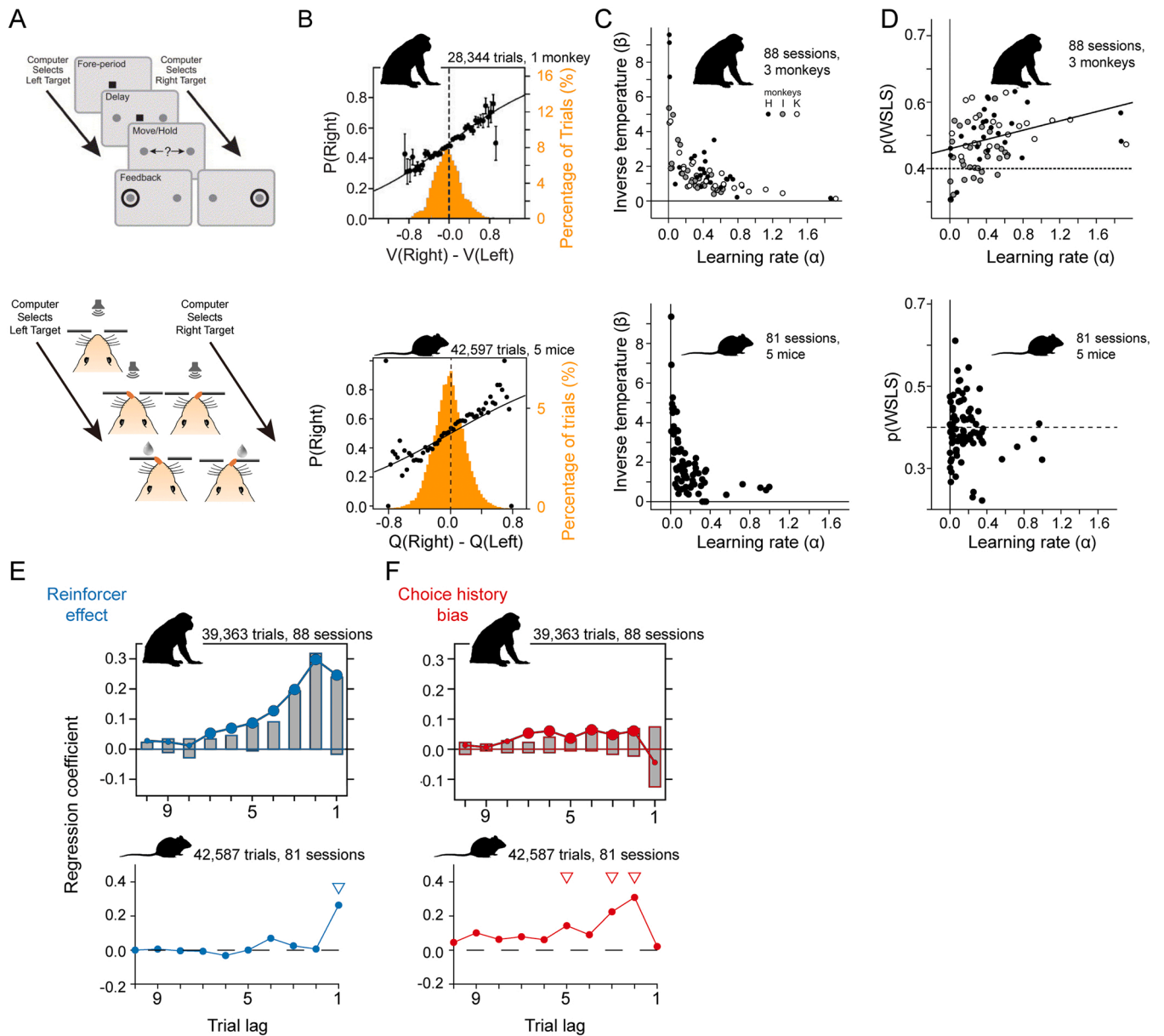


Fig. 2. Performance of monkeys and mice in matching pennies. (A) Behavior paradigm for monkey and mouse. Top: monkeys use saccade to indicate the decisions on computer screen. Bottom: mice use tongue-licking to indicate the decisions and get water reward from the licking port. (B) Psychometric curve of the behavior of monkeys (Lee et al., 2004) and mice (Wang et al., 2022) determined by fitting similar reinforcement learning-based computational models. Orange histograms represent the distribution of trials according to the difference of action values, which are variables related to action selection. Black curves represent the predicted behavior by the model. Black dots represent the observed behavior in actual experiment. (C) Model estimations of learning rate (latent parameter that modulates the strength of influence of most recent outcome on behavior) and inverse temperature (modulates the variability of behavior) of monkey data (Seo et al., 2009) and mouse data (Wang et al., 2022). (D) The probability of animals adopted win-stay-loose-switch strategy plotted against the estimated learning rate of monkey data (Seo et al., 2009) and mouse data (Wang et al., 2022). (E) Logistic regression coefficients relating the reinforcer effect bias with the current choice of monkey data (Seo et al., 2009) and mouse data (Wang et al., 2022). (F) Logistic regression coefficients relating the choice history bias with the current choice of monkey data (Seo et al., 2009) and mouse data (Wang et al., 2022).

play matching pennies with subtle differences, such as the higher reliance on short-term choice history in rodents. Furthermore, the analyses show that although animals can play matching pennies at close to Nash equilibrium, there is residual bias due to the reinforcer effect, where the subject is more likely to select the previously rewarded option in accordance with reinforcement learning.

3.2. Rock-paper-scissors

Rock-paper-scissors, the timeless children’s game, is another example of a competitive, zero-sum game, where each player decides

simultaneously whether to choose rock, paper, or scissors (Fig. 1B). The Nash equilibrium is to choose the three options randomly with equal probabilities. Unlike matching pennies, the logic for determining the winning action in rock-paper-scissors is circular, which may require advanced cognitive abilities to comprehend (Astur and Sutherland, 1998), though it is also possible to play without full knowledge of the logic. Macaques can play the iterated version of both unbiased and biased rock-paper-scissors against computer opponents with varying competitive pressure (Abe and Lee, 2011; Lee et al., 2005). Like matching pennies, macaques adapted to the increasing pressure by adjusting their choice strategy to maintain the reward rate. The animals’

performance in rock-paper-scissors was decent but less than ideal because they systematically favored the action that would have won in the previous trial, at a rate higher than that predicted by the Nash equilibrium.

3.3. Inspection game

The inspection game models a situation where the inspector verifies if the inspectee follows regulations, such as an employer can choose whether to check if an employee is working, while the employee can decide whether to work or shirk. The employer gains the most by not inspecting while the employee works. By contrast, the employee gains the most by shirking without being inspected. The game can be formalized into a payoff matrix by setting i to be the cost of the inspection, f to be the cost of the inspectee to comply with the rules, and b to be the punishment on the inspectee for being caught with illegal behavior (Fig. 1C). For the inspectee, complying with the rules is the safe choice, since the outcome is guaranteed, independent of the inspector's choice. Counterintuitively, the Nash equilibrium for the inspector does not depend on the cost of inspection, which instead affects the inspectee's Nash equilibrium, given by the equations:

$$P_{\text{inspector,control}} = \frac{c-g}{b+c}; P_{\text{inspectee,legal}} = 1 - \frac{i}{b} \quad (2)$$

Macaques followed mostly the theoretical prediction when playing the game as the inspectee with a computer opponent (Dorris and Glimcher, 2004). In this study, the computer was programmed to adopt a reinforcement learning algorithm to predict the animal's future choice and act accordingly to maximize payoff. Varying the cost of inspection altered the macaque's choice behavior, even though it should not affect the animal's payoff, as the theory predicted. Notably, the behavior of the animal deviated from the Nash equilibrium: they preferred the safe option when the inspection cost was high, but the preference switched to the risky option when the inspection cost was low. The deviation was attributed to the discrepancy between subjective and objective values as well as value for information seeking, because the animal could only gain information about the opponent's action by choosing the risky option.

4. Cooperative games

Animals may cooperate to attain a shared objective. For instance, hunting in groups can improve the likelihood of success for all individuals involved. Helping a near relative may increase the fitness of the genes carried by the individual (Lehmann and Rousset, 2014). Likewise, interspecific mutualism can benefit both parties in their fitness (Boucher et al., 1982). In addition, animals are known to help other individuals without immediate reward, through interactions such as reciprocal altruism (Trivers, 1971), pseudo-reciprocity (Connor, 1986), by-product mutualism (Dugatkin, 2002), and group selection (Wilson, 1975). A set of games have been proposed to model these situations in which the players must balance between cooperative and competitive strategies. Compared to purely adversarial games, there is typically a stronger incentive to understand the opponent's strategy in cooperatives games.

4.1. Prisoner's dilemma

Prisoner's dilemma presents a scenario where two prisoners choose to cooperate or defect. The prisoners would serve short sentences if they both cooperate or moderate sentences if they both defect. However, one could walk free by defecting if the other player cooperates and serves a long sentence, known as temptation (defect on a cooperated opponent) and sucker (cooperate when the opponent defects) trials (Fig. 1D). For a one-shot game of prisoner's dilemma, the rational move is to defect because regardless of the opponent's choice, defection always yields a

better outcome. For an iterated game, the Nash equilibrium is also to defect repeatedly if the players know when the game will end. Yet if the players are uncertain about the length of the game, mutual cooperation leads to a better payoff. There are multiple strategies to play iterated prisoner's dilemma with infinite turns, such as bookkeeping or cost-counting, which use the information of past turns to inform the current decision (Raihani and Bshary, 2011). Tit-for-tat is one instance of bookkeeping that promotes long-term cooperation, referring to the strategy that the player copies the last move of its opponent. Another common strategy is alternating reciprocity, where players take turns exploiting the high payoff of temptation trials.

A recent study examined the performance of a pair of macaques in iterated prisoner's dilemma (Haroush and Williams, 2015). In general, the monkeys preferred to defect, yet deviated from the Nash equilibrium by choosing cooperation more often than predicted, adopting a mix of tit-for-tat and win-stay-lose-switch strategies. Interestingly, when pitted against computer opponents designed to mimic the animals' behavior, the macaques cooperated significantly less, even on trials following mutual cooperation. Cooperation was also reduced when monkeys played with each other, albeit in separate rooms so the identity of the opponent was not known. Moreover, in a related game, cooperative behavior could be encouraged if animals were shown such strategies in prior encounters (Moeller et al., 2023; Unakafov et al., 2020). Collectively, the implication is that playing against a real conspecific influences the macaque's choice behavior in a cooperative game.

Chimpanzees have been tested on iterated prisoner's dilemma. The behavioral results were inconsistent with predictions by game theory, perhaps due to the sequential design of the task (Hall et al., 2019). On average, animals chose cooperation with a high probability. Counterintuitively, the follower animal defects less than expected, even when its opponent defected first, resulting in poor payoff. The chimpanzees formed pairs voluntarily to play in the study, therefore the players could have existing relationships to explain the seemingly altruistic behavior. Two species of New World monkeys, capuchins (*Sapajus [Cebus] apella*) and squirrel monkeys (*Saimiri boliviensis*), have also been trained to play iterated prisoner's dilemma sequentially (Smith et al., 2019; Vale et al., 2019). Neither species settled on a specific strategy. They either played randomly, were biased towards one option, or matched the opponent's action. The same pairs of animals were then trained for more sessions, resulting in further consolidation of previous tendencies. A summary analysis across sessions for all animals suggested a shift towards the Nash equilibrium of mutual defection, implying the potential to eventually learn the game after extensive training.

Rats exhibited an overall preference for mutual defection in iterated, sequential prisoner's dilemma (Gardner et al., 1984), which accentuated further when the game became simultaneous. In this study, two rats were placed in different T-mazes. Each animal chose to turn either left or right at the intersection of the maze, which corresponded to cooperation and defection, respectively. The payoffs were designed to emulate the prisoner's dilemma: animals received 3 food pellets when both playing cooperation, 1 pellet when both playing defection, and 5 and 0 pellets respectively when one defected and the other cooperated. In sequential sessions, the T-mazes were placed face-to-face so that the animal could see the other's action when they ran down the track. The probability to defect increased upon training when the opponent started by cooperating, indicative of strategic play. When playing against a random or tit-for-tat strategy sequentially (Viana et al., 2010), the rats would still sometimes opt for cooperation against the random strategy or adopt a mixture of mutual cooperation and alternating reciprocity against tit-for-tat. Therefore, their behaviors deviate from the optimal solutions of always defecting for random strategy and cooperating for tit-for-tat. Meanwhile, decreasing the payoff for mutual cooperation while maintaining the payoff of temptation trial led to fewer mutual cooperation without affecting the alternation between temptation and sucker trials, suggesting that the animals were sensitive to changes in the payoff matrix. In a simultaneous game, the rats showed a high level of

cooperation without evidence of utilizing either tit-for-tat or win-stay-lose-switch strategies (Wood et al., 2016). When playing against opponents adopting different strategies, rats cooperated more often against tit-for-tat than win-stay-lose-switch or random strategies (Donovan et al., 2020).

On the contrary, birds playing prisoner's dilemma showed a low level of cooperation (Clements and Stephens, 1995; Stevens, 2004). The birds were put in different chambers with two keys for pecking to indicate either cooperation or defection. Based on their choices, food pellets were distributed similarly as the rat study to mimic the prisoner's dilemma. Blue jays (*Cyanocitta cristata*) started by playing mostly mutual cooperation, then gradually shifted to predominantly mutual defection. Similar to rats, blue jays did not employ tit-for-tat or win-stay-lose-switch strategy. However, the birds tended to repeat their own last choice. Pigeons defected at the same rate in iterated prisoner's dilemma in several studies (Baker and Rachlin, 2002; Green et al., 1995; Sanabria et al., 2003). The birds chose mostly to defect when playing against a computer opponent following a tit-for-tac strategy. However, the animal would play cooperation more often if such choice or outcome was strengthened by shortening the intertrial interval or pairing the previous choice by salient sensory input (Baker and Rachlin, 2002). Increasing the overall payoff proportional to the fraction of cooperation choice caused more cooperative decisions (Sanabria et al., 2003). These results suggested that birds rely more on the immediate payoff, with a steep temporal discount (Kagel et al., 1986), in decision-making during cooperative games. Altogether, these results reveal a range of strategies and preferences for defection versus cooperation, which depend on factors including species, simultaneity of play, outcome sizes, and the opponent identity.

4.2. Assurance

Assurance game, also known as trust dilemma, stag hunt, or common interest, imitates the case where two hunters decide separately whether to hunt a stag or a hare. It takes the hunters' joint efforts to successfully hunt the larger stag, but one hunter can catch the smaller hare alone (Fig. 1E). Two pure-strategy Nash equilibria exist in the assurance game: a payoff-dominant one where players choose to hunt stag to maximize the payoff; and a risk-dominant one where players hunt hare separately to minimize the risk. In addition, there is a mixed-strategy Nash equilibrium to choose stag with the probability of:

$$P_{stag} = \frac{d - c}{a + d - b - c} \quad (3)$$

In general, Old World monkeys performed better than New World monkeys in the assurance game. Macaques have been tested with both simultaneous and sequential versions of the game (Brosnan et al., 2012). Animals were trained first on either the simultaneous or sequential game, then switched to the other version, therefore avoiding confounds that may associate with initial learning from one version of the game. Macaques successfully found the payoff-dominant Nash equilibrium of stag-stag shortly in both versions of the game. Moreover, they adjusted their behavior for better payoffs when facing computer players with varying probabilities to choose stag (Parrish et al., 2014). By contrast, capuchin monkeys could not find any Nash equilibrium when interacting directly with the experimenter (Brosnan et al., 2011; Brosnan et al., 2012), though they did well in computerized simultaneous game, favoring the stag-stag strategy most of the time (Brosnan et al., 2012; Smith et al., 2019). Notably, the poor performance occurred regardless of previous experience in the game. Another study implemented a biased payoff matrix for the capuchins, in which one player would get twice the reward as the other player (Robinson et al., 2021). The capuchins favored the stag-stag option, yet with a strong dependence on the quality of the reward. Similarly, squirrel monkeys significantly preferred the payoff-dominant equilibrium (Vale et al., 2019). In comparison, rats played according to both Nash equilibria without preference when

playing against a computer-controlled stooge rat that employed a tit-for-tat strategy (Donovan et al., 2020).

The behavior of chimpanzees was variable in the assurance game (Brosnan et al., 2011). In the sequential game, some pairs found the payoff-dominant strategy, while most pairs generally matched their partner's choice, without a preference for either equilibrium. Additionally, some animals behaved indistinguishable from chance. The two pairs of chimpanzees preferring the payoff-dominant strategy were tested in a simultaneous version later. Only one pair continued to choose stag-stag, while the other pair did not. When novel tokens were introduced, both pairs adopted the stag-stag option. A subsequent study reported that chimpanzees were unable to play the assurance game with any preference (Hall et al., 2019). However, in more ecological-relevant setups, chimpanzees displayed more cooperative behaviors (Bullinger et al., 2011; Duguid et al., 2014). In high-risk situations where the payoff of hare is relatively high, chimpanzees reduced their stag-stag coordination. By contrast, in low-risk situations, they adopted a leader-follower strategy in which one animal took the risk of the stag first to encourage the other player to follow. Overall, these contradictory results suggested that the animals may not fully understand the game and its payoff matrix, because most of them simply played a matching strategy, instead of exploring to maximize their payoff. Intriguingly, the pairs that played stag-stag also performed the best in other cognitive tasks (Brosnan et al., 2011), suggesting that more training could result in more consistent behavior and convergence of more reasonable strategies.

4.3. Snowdrift

The snowdrift game, also known as the game of chicken or hawk-dove game, represents the situation where the players share a common goal, yet they could choose to cooperate or defect for free riding. A common analogy is the situation of two drivers deciding whether to shovel a snow-blocked road, hence the name snowdrift. If both players decide not to shovel, no one will benefit. If one decides to shovel, then the other gets a freeride for a better outcome. Otherwise, they can shovel the road together and split the labor, which results in mutual benefit (Fig. 1F). There are multiple Nash equilibria for the snowdrift game: two pure strategies in which one player always chooses one option and the other player always chooses the other option; and a mixed strategy (Correia and Stoof, 2019) where both players choose to shovel with a probability of:

$$P_{cooperate} = \frac{s}{t + s - 1} \quad (4)$$

The pure equilibria are only reached in a sequential setup; hence the mixed equilibrium is the optimal solution in a simultaneous game. Players may favor free riding, which carries the risk of mutual destruction if no one pays the cost. Therefore, other common strategies are bookkeeping and alternating reciprocity. Unlike the prisoner's dilemma, the player can always avoid the worst-case outcome by playing cooperation.

Macaques found the pure Nash equilibria in sequential snowdrift game (Brosnan et al., 2017; Ong et al., 2021). They settled on one animal always playing one role. When they played the simultaneous game, the monkeys failed to reach any Nash equilibrium (Brosnan et al., 2017). Furthermore, there is evidence that animals utilized both sensory information and strategic inference to predict the opponent's behavior, which was sensitive to the social rank of the players (Ong et al., 2021). Capuchins found the pure-strategy equilibria in sequential game yet failed in simultaneous game as well (Smith et al., 2019). Specifically, it was surprising that an animal's role does not depend on the relative social rank of the pair, since the same pair could switch their roles in a different session, suggesting that the roles might be determined by chance. The animal that started by playing defection would do well in the game, because the animal that followed by playing cooperation

would receive less reward if it switched to defection; therefore, it would revert to cooperation. While this is an optimal solution, it is unclear if the animals fully explored the action-outcome space. While the capuchins developed individual preference toward one action, the player that made the second decision tended to choose the action different from the first player, especially when the first mover already picked defect, presumably to avoid mutual destruction (Smith et al., 2019). Unlike other primates, squirrel monkeys failed to find any Nash equilibrium in a sequential game (Vale et al., 2019). Some individuals preferred cooperation, which was not exploited by their opponents who chose randomly. Note that these animals were trained to play the snowdrift game along with the assurance game and the prisoner's dilemma simultaneously. Therefore, the animals could be confused by the changing payoff contingencies across different games.

Chimpanzees can work together in group hunting (Boesch, 2002), albeit they preferred working alone when cooperation yielded no better outcome (Bullinger et al., 2011). In sequential snowdrift game, chimpanzees cooperated most of the time (Sánchez-Amaro et al., 2016). The length of the decision period and the labor cost to make a choice were manipulated to apply different pressures and alter the payoff matrix of the game. Assuming both animals were rational players, they should try to minimize their cost by waiting until the last moment for the other player to cooperate first, even more so in the trials with a higher decision cost and longer decision window. In practice, the animals did wait longer in trials with a larger cost, although the response time was far shorter than the decision window, and the first actor tended to pay more effort. Furthermore, the animal's decision was not affected by the other player's action in the previous trial. The result could be due to an aversion for the animal to losing a reward or insensitivity to the effort, so the animals reacted quickly to secure the reward. Contradictory result was reported in another study, showing that chimpanzees had no preference in cooperation or defection, nor was the second decision significantly influenced by the first decision (Hall et al., 2019). Furthermore, Sánchez-Amaro et al. adopted a social dilemma that resembled the snowdrift game, introducing fake moves in the decision-making process (Sánchez-Amaro et al., 2019). The player could pretend to cooperate first, tricking the other player into cooperation, then switch to defection to get a free ride. A rational player here could adopt a more complex strategy like deception, in addition to typical strategies in a normal snowdrift game. The animals tended to compete with each other by waiting longer to act or deceiving the opponents with fake cooperation. Pigeons preferred cooperation in a simultaneous snowdrift game against computer opponents and implemented tit-for-tat or random strategies (Green et al., 1995). However, the study focused on the prisoner's dilemma and did not conduct a thorough analysis of the behavior in the snowdrift game.

5. Other games

5.1. Ultimatum, dictator, and equal split

In ultimatum, one player called the proposer is endowed with a sum of reward. The proposer suggests a ratio to split of the reward with another player, called the responder. If the responder accepts the offer, they split the reward as proposed. However, if the responder rejects the offer, both players receive no reward (Fig. 1G). A rational responder should accept any offer great than zero to maximize its own payoff. Similarly, the proposer should always propose a minimum amount. The dictator game is a derivative of the ultimatum game, where one player called the dictator makes a final decision on how to split the reward (Fig. 1H). It is impractical to teach animal to play the ultimatum game since the decision space is too large for the proposer. Instead, the equal-split game simplifies the decisions into discrete sets of proportions to split the food. The proposer chooses among these discrete offer options, and the responder decides whether to reject it.

Non-human primates showed inconsistent behavior across different

studies with various task designs. Chimpanzees and bonobos (*Pan paniscus*) acted rationally in general, selecting the options that maximized the proposer's outcome, with the responder accepting unfair (the proposer gets more) offers most of the time (Kaiser et al., 2012) while rejecting hyper-unfair (the responder gets zero) offers reliably. However, another study showed that chimpanzee proposers started by choosing more selfish splits, then gradually switched to more equal offers (Proctor et al., 2013). Nevertheless, the responder accepted any offer irrespective of the fairness. When the same animals were also tested on the dictator game, the proposer chose equal split significantly less. Taken together, these results suggested that chimpanzees acted sensibly but did not fully maximize payoff, at least when it played as proposer.

5.2. Trust game

In the trust game, the first player called the trustor is given a reward worth X . The trustor is free to give up a fraction q of the reward, which is magnified by a factor K before being given to another player, the trustee. The trustee then decides whether to return a fraction p of the received reward to the trustor, in exchange for the generosity (Fig. 1I). To maximize the total payoff, the trustor should transfer all the reward to the trustee because of the magnification factor. However, it is up to the trustee to decide whether to honor the endowment and pay the trustor back.

Like ultimatum, the trust game has been simplified for animals to play (Engelmann et al., 2015). The trustor can choose no-trust or trust, resulting in getting a low-quality reward immediately or sending a high-quality reward to the trustee respectively. If the trustee receives the high-quality reward, it may then decide whether to send a part of the reward back. Note that regardless of the trustee's decision, it has no access to the reward that could be sent back, which discourages the trustee to exploit the trust. The chimpanzees chose to trust conspecifics in general, and they adjusted their behavior according to the other player's history and their relationship (Engelmann and Herrmann, 2016; Engelmann et al., 2015).

6. Neural circuits involved in game play

Most studies reviewed so far focused on quantifying behavior. In several pioneering works, neural measurements were made during game play, allowing the researchers to link neural activity to behavioral performance, highlighting the potential to uncover neural correlates underlying flexible and strategic decision-making.

As the prototypical competitive game, matching pennies requires the animal to avoid being exploited by the opponent, while also acting to gain rewards by predicting the opponent's choice. Hence, matching pennies is suitable for studying the neural mechanisms responsible for behavioral variation and the modeling of the opponent. Early studies in macaques have shown that neurons in dorsolateral prefrontal cortex and lateral intraparietal cortex encoded task-related variables such as choice and reward history, as well as latent variables involved in the estimation of the expected outcome (Barraclough et al., 2004; Seo et al., 2007). Furthermore, neural activity in the cortex was linked to strategy. The dorsomedial prefrontal cortex and supplementary eye field contained neural signals indicating a switch from a previously preferred choice (Donahue et al., 2013; Seo et al., 2014), while neural activity in dorsolateral prefrontal cortex and orbitofrontal cortex was correlated with the actual outcome and hypothetical outcomes of unchosen actions (Abe and Lee, 2011). This neural representation for the outcome of unselected choices, also known as fictive reward, may be particularly important for rapid learning as indicated by efforts to teach artificial intelligence to play games by including counterfactual reasoning of alternative possibilities of past events (Bakhtin et al., 2022; Brown and Sandholm, 2018; Moravčík et al., 2017). Meanwhile, the superior colliculus represented the upcoming choice and action values, while

stimulating neurons in the superior colliculus promoted the selection of contralateral choices (Thevarajah et al., 2010). Taken together, these findings outlined a cortical-tectal brain network underlying competitive behavior in primates.

Rodent studies have provided additional insights into the greater brain circuitry involved by illuminating the functions of striatum and neuromodulatory systems in regulating flexible behavior during matching pennies. Rats with dorsolateral striatum lesions were less sensitive to reward and exhibited repetitive behavior in matching pennies (Skelin et al., 2014). However, the same study showed that damaging dorsolateral or dorsomedial striatum did not fully abolish the mixed-strategy behavior, suggesting the involvement of other neural systems. Indeed, activating noradrenergic inputs from locus coeruleus into rat anterior cingulate cortex promoted the animals to pursue stochastic behavior (Teruo et al., 2014). Our lab's recent study demonstrated that pupil transients signaled multiple task-related variables including choice, outcome, as well as reward prediction error, suggesting phasic arousal-linked neuromodulatory activity correlated to trial-to-trial performance during flexible behavior (Wang et al., 2022).

The literature on neural mechanisms underlying cooperative games is limited. It was discovered that distinct subpopulations of neurons in the dorsal anterior cingulate cortex encoded the animal's predictions of the opponent's upcoming choice and its own decisions (Haroush and Williams, 2015). Disruption of the neural activity in this region selectively inhibited cooperation that normally occurred after a recent positive payoff. Neural activities correlated with modeling of the opponents, along with previous choice and outcome, were found in the medial superior temporal sulcus of monkey playing a variation of the snowdrift game (Ong et al., 2021).

These results revealed only the tip of the iceberg into a likely complex and distributed neural circuitry involved in implementing and inferring the strategies of self and others for making social decisions (Fig. 3). Further studies leveraging behavioral, neural, and computational approaches are needed to clarify how neural circuits can compute, arbitrate, deploy, and evaluate strategic decisions during social games.

7. Caveats in experimental design and future directions

Studies to date provided compelling evidence that many species can understand action-outcome contingencies and make strategic moves in different social games. Select experiments further revealed some of the neural correlates underlying such behavior. However, there were instances of seemingly contradictory reports on behavioral responses to the same games, underscoring the importance of experimental design when using games to study social behavior.

Motivation is a vital factor that affects performance. For studies of

some non-human primates such as chimpanzees (though with the notable exception of macaques), the common practice is to provide ad libitum food and water, which reduced the motivation of the animals to maximize rewards. Food availability substantially affected the strategic behavior of rodents (Viana et al., 2010; Wood et al., 2016), while food rewards with different values altered the behavior of primates (Robinson et al., 2021). Manipulating the amount of reward suggested that the animal would improve their performance with higher rewards (Viana et al., 2010). Therefore, it is important to ensure that the rewards are meaningful throughout a session to maintain a consistently high level of motivation during game play.

Another essential factor is the equipment. To accommodate different species, many kinds of operandum were used for indicating choices, such as saccade, token, or rope-pull for primates, and joystick, tongue-lick, or nose-poke for rodents. In some cases, the game is fully automated with a computer managing reward or token delivery, while in other cases the human experimenter actively manages the game, i.e., exchanging tokens with the chimpanzees. The specific implementations could introduce biases and skew results. Future studies should strive for more stable behavioral readouts by adopting a computerized interface to manage the game and using abstract operanda for indicating responses. For instance, touchscreens can be used by different animal species for behavioral testing (Dumont et al., 2021; Palmer et al., 2021; Shepherd et al., 2016; Sullivan et al., 2021). Moreover, animals behaved differently in simultaneous and sequential games. Although different strategies might be achieved by testing the two game modes, sequential games often led to behaviors that did not appear strategic (Hall et al., 2019; Smith et al., 2019; Vale et al., 2019). Hence simultaneous games are more likely to push animals to their limit of strategic inference.

There were aspects of behavior that were not explained by game theory. For example, the chimpanzee matcher responded faster than the mismatcher in matching pennies, despite of the symmetric payoff matrix. Other study indicated that whether the animal had to move (active choice) versus do nothing until a timeout (passive choice) to indicate the same choice could make a difference in the behavior (Guitart-Masip et al., 2014). Across studies and species, these effects often depended on the task implementation and the specific causes should be clarified by performing control experiments. Transparent game model was developed to describe the situation where the player has a certain probability to observe the opponent's choice before making its own (Moeller et al., 2023; Unakafov et al., 2020). The model predicted less cooperation in an iterated prisoner's dilemma, which could explain the lack of cooperative decision in some published accounts of animal behavior (Gardner et al., 1984; Hall et al., 2019; Haroush and Williams, 2015). These idiosyncrasies are detected as deviations after quantitative modeling of the behavior; they are worth further investigation as they can reflect

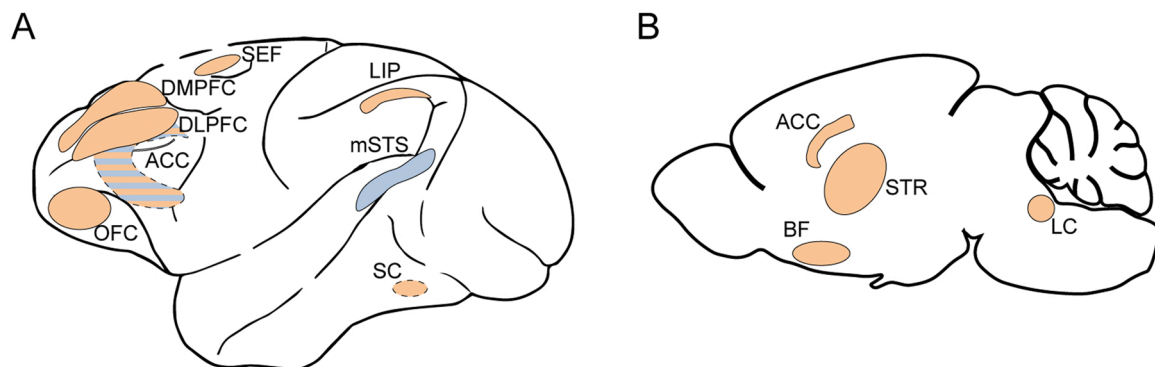


Fig. 3. Brain regions related to social games and strategic behavior.

(A) Lateral view of macaque brain with regions involved in competitive game (yellow) and cooperative game (blue). ACC: anterior cingulate cortex. DLDFC/DMPFC: dorsolateral/dorsomedial prefrontal cortex. LIP: lateral intraparietal cortex. mSTS: medial superior temporal sulcus. SC: superior colliculus. SEF: supplement eye field. (B) Sagittal view of mouse brain with regions involved in competitive game. ACC: anterior cingulate cortex. BF: basal forebrain. LC: locus coeruleus. STR: striatum.

intrinsic properties of the motor and cognitive systems.

Notwithstanding a few notable exceptions such as macaques and rodents playing matching pennies over thousands of trials, many studies reported behaviors of animals playing games without extensive training. Unlike human players who can learn through verbal instructions, animals grasp the game rules based on trial-and-error. Moreover, learning may be slowed because the requisite stimulus-action associations (e.g., directional tongue licks in rodents) are often implausible in the natural world, away from typical neural repertoire of the animals (Guitart-Masip et al., 2014; Meister, 2022). Therefore, some of the reported behaviors in the literature could arise from insufficient learning, consistent with several studies showing that animal's performance could be improved upon further training (Smith et al., 2019; Vale et al., 2019). Therefore, future studies should aim at finding the end-point strategy when the behavior settles to set a solid foundation for the behavioral and neural analyses.

A promising direction is to investigate how animals behave when facing conspecifics versus computer opponents. Playing against a conspecific may be a better approximation of actual social decisions. There is emerging evidence that monkeys and rodents would exhibit pro- or anti-social choices for other animals that are otherwise absent (Chang et al., 2013; Haroush and Williams, 2015; Hernandez-Lallement et al., 2014; Marquez et al., 2015). Yet computer opponents can be implemented to play any policy to test how animal responds to varying strategies. Additionally, it may be difficult for two animals to learn the payoff matrix from scratch in an unsupervised manner. A middle ground may be that computer opponents could guide the initial learning before game play between conspecifics. One limitation of games is that some aspects of social interactions are not captured, such as social touch which may influence the decision-making process.

During games, animals are incentivized to perform strategically with consideration of the opponent's actions, but alternatively it is possible that some species particularly rodents are acting based on simple instrumental choice-outcome associations. There are several lines of evidence to indicate that rodents can act strategically. When presented with opportunities to reward self only versus self and others, rats would choose mutual reward indicating pro-social behavior beyond simple reinforcement-based learning (Hernandez-Lallement et al., 2014; Marquez et al., 2015). The degree of pro-social behavior depends on prior social experience but not the strain of the conspecific (Ben-Ami Bartal et al., 2014). These findings in the lab are consistent with behavioral repertoire in nature, where rats can discern between kin and non-kin to cooperate and share food (Schweinfurth, 2020). Importantly, series of studies have found quid pro quo behavior demonstrating direct reciprocity in which the decision to give food is based on prior experience of receiving donations (reviewed in (Schweinfurth, 2020)). Therefore, there are ample data to suggest that rodents can interact with conspecifics strategically, although explicit evaluation of this trait during the setting of a competitive or cooperative game remains to be tested.

Teaching animals to play games has revealed insights into the decision-making process in a social context. The range of competitive and cooperative games offers a variety of lenses to tease out various components of flexible and strategic behavior. The current literature has clearly demonstrated that games are amenable to animal models including macaques and mice, for which molecular, electrophysiological, and imaging methods have enabled large-scale recording of neural dynamics. Specifically for games, the prospect of identifying neural correlates is high because the behavioral performance can be understood through rigorous frameworks built on game theory and reinforcement learning. For these reasons, we expect games will continue to have a central position in the field of neuroscience for studying the brain mechanisms underlying social interactions and strategic behavior.

Declaration of Interests

Authors report no conflict of interest.

Data Availability

No data was used for the research described in the article.

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