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Game theory and neural basis of social decision making

Daeyeol Lee

Decision making in a social group has two distinguishing features. First, humans and other animals routinely alter their behavior in response to changes in their physical and social environment. As a result, the outcomes of decisions that depend on the behavior of multiple decision makers are difficult to predict and require highly adaptive decision-making strategies. Second, decision makers may have preferences regarding consequences to other individuals and therefore choose their actions to improve or reduce the well-being of others. Many neurobiological studies have exploited game theory to probe the neural basis of decision making and suggested that these features of social decision making might be reflected in the functions of brain areas involved in reward evaluation and reinforcement learning. Molecular genetic studies have also begun to identify genetic mechanisms for personal traits related to reinforcement learning and complex social decision making, further illuminating the biological basis of social behavior.

Decision making is challenging because the outcomes from a particular action are seldom fully predictable. Therefore, decision makers must always take uncertainty into consideration when they make choices[1]. In addition, such action-outcome relationships can change frequently, requiring adaptive decision-making strategies that depend on the observed outcomes of previous choices[2]. Accordingly, neurobiological studies on decision making have focused on the brain mechanisms involved in mediating the effect of uncertainty and improving decision-making strategies by trial and error. Signals related to reward magnitude and probability are widespread in the brain and are often modulated by decision making[3–9]. Some of these areas might be also involved in updating the preference and strategies of decision makers[10–14].

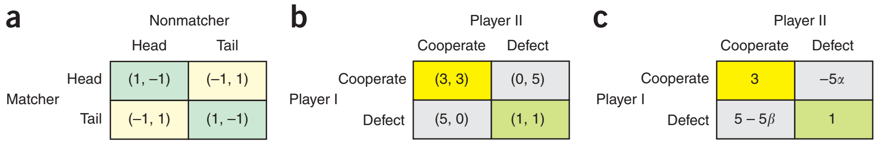
Compared to solitary animals, animals living in a large social group face many distinctive challenges and opportunities, as reflected in various cognitive abilities in the social domain, such as communication and other prosocial behaviors[15]. This review focuses on the neural basis of socially interactive decision making in humans and other primates. The basic building blocks of decision making that underlie the processes of learning and valuation also are important for decision making in social contexts. However, interactions among multiple decision makers in a social group show some additional features. First, behaviors of humans and animals can change frequently, as they seek to maximize their self-interest according to the information available from their environment. This makes it difficult to predict the outcomes of a decision maker's actions and to choose optimal actions accordingly. As a result, more sophisticated learning algorithms might be required for social decision making[16,17]. Second, social interactions open the possibilities of competition and cooperation. Humans and animals indeed act not only to maximize their own self-interest, but sometimes also to increase or decrease the well-being of others around them. These aspects of social decision making are reflected in the activity of brain areas involved in learning and valuation.

Game theory and social preference

A good starting point for studies of social decision making is game theory[18]. In its original formulation, game theory seeks to find the strategies that a group of decision makers will converge on, as they try to maximize their own payoffs. Nash equilibrium refers to a set of such strategies from which no individual players can increase their payoffs by changing their strategies unilaterally[19]. In a two-player competitive game known as matching pennies (**Fig. 1a**), for example, each player can choose between two alternative options, such as the head and tail of a coin. One of the players wins if both players choose the same option and loses otherwise. For the matching-pennies game with a symmetrical payoff matrix (as in **Fig. 1a**), the Nash equilibrium is to choose both options with the same probabilities. Any other strategy can be exploited by the opponent and therefore reduces the expected payoff. In both humans and nonhuman primates, however, the predictions based on the Nash equilibrium are often systematically violated for such competitive games[17,20,21]. As discussed below, this might be due to various learning algorithms used by the decision makers to improve the outcomes of their choices iteratively.

How game theory can be used to investigate cooperation and altruism is illustrated by a well known game, the prisoner's dilemma. The two players in this game can each choose between cooperation and defection. Each player receives a higher payoff by defecting, whether the other player chooses to cooperate or defect, but the payoff to each player is higher for mutual cooperation than for mutual defection, hence creating a dilemma (**Fig. 1b**). If this game is played only once and the players care only about their own payoffs, both players should defect, which corresponds to the Nash equilibrium for this game. In reality and in laboratory experiments, however, both these assumptions are frequently violated.

Yale University School of Medicine, Department of Neurobiology, 333 Cedar Street, SHM B404, New Haven, Connecticut 06510, USA. Correspondence should be addressed to D.L. (daeyeol.lee@yale.edu).



a

		Nonmatcher	
		Head	Tail
Matcher	Head	(1, –1)	(–1, 1)
	Tail	(–1, 1)	(1, –1)

b

		Player II	
		Cooperate	Defect
Player I	Cooperate	(3, 3)	(0, 5)
	Defect	(5, 0)	(1, 1)

c

		Player II	
		Cooperate	Defect
Player I	Cooperate	3	-5α
	Defect	$5 - 5\beta$	1

Figure 1 Payoff matrix for the games of matching pennies and prisoner's dilemma. (**a**) For the matching-pennies game, a pair of numbers within each pair of parentheses indicates the payoffs to the matcher and nonmatcher, respectively. Blue or yellow rectangles indicate the outcomes favorable to the matcher or nonmatcher, respectively. (**b**,**c**) The prisoner's dilemma game. (**b**) A pair of numbers within the parentheses indicates the payoffs to players I and II, respectively. The yellow and green rectangles correspond to mutual cooperation and mutual defection, respectively, whereas the gray rectangles indicate unreciprocated cooperation. (**c**) Player I's utility function adjusted according to the model of inequality aversion. The values of α and β indicate the sensitivity to disadvantageous and advantageous inequality. For $\beta > 0.4$, mutual cooperation becomes a Nash equilibrium.

Games can be played repeatedly, often among the same set of players. This makes it possible for some players to train others to deviate from the equilibrium predictions for one-shot games. In addition, humans often cooperate in prisoner's dilemma games, whether the game is one-shot or repeated[22]. Therefore, for humans, decision making in social contexts may not be entirely driven by self-interest, but at least partially by preferences regarding the well-being of other individuals. Indeed, cooperation and altruistic behaviors abound in human societies[23] and may also occur in nonhuman primates[24–26]. In theory, multiple mechanisms—including kin selection, direct and indirect reciprocity and group selection—can increase the fitness of cooperators and thus sustain cooperation[23,27]. Punishment of defectors or free-riders at a cost to the rule enforcer, often referred to as altruistic punishment, also effectively deters defection[23,28–30].

In economics, the subjective desirability of a particular choice is quantified by its utility function. Although the classical notion of utility only concerns the state of the decision maker's individual wealth, the utility function can be expanded, when people take into consideration the well-being of other individuals, to incorporate social preference. For example, the utility function can be modified by the decision maker's aversion to inequality[31]. For two-player games, the first player's utility, $U_1(x)$, for the payoff to the two players $x = [x_1\ x_2]$, can be defined as follows:

$$U_1(x) = x_1 - \alpha I_D - \beta I_A$$

where $I_D = \max\{x_2 - x_1, 0\}$ and $I_A = \max\{x_1 - x_2, 0\}$ refer to inequalities that are disadvantageous and advantageous to the first player, respectively. The coefficients α and β indicate sensitivities to disadvantageous and advantageous inequalities, respectively, and it is assumed that $\beta \leq \alpha$ and $0 \leq \beta < 1$. Therefore, for a given payoff to the first decision maker, x_1, $U_1(x)$ is maximal when $x_1 = x_2$, giving rise to the preference for equality. When the monetary payoff in the prisoner's dilemma is replaced by this utility function with the value of β sufficiently large, mutual cooperation and mutual defection both become Nash equilibria[32] (**Fig. 1c**). When this occurs, a player cooperates as long as he or she believes that the other player will cooperate as well.

Evidence for altruistic social preference and aversion to inequality is also seen in other experimental games, such as the dictator game, the ultimatum game and the trust game[17,32], and their possible neural substrates have been examined[33]. In the dictator game, a dictator receives a fixed amount of money and donates a part of it to the recipient. This ends the game, so there is no opportunity for the recipient to retaliate. Any amount of donation reduces the payoff to the dictator, so the amount provides a measure of altruism. During dictator games, people tend to donate on average about 25% of their money[17].

An ultimatum game is similar to the dictator game in that one of the players (proposer) offers a proportion of the money to the recipient, who now has the opportunity to reject the offer. If the offer is rejected, neither player receives any money. The average offer in ultimatum games is about 40%, significantly higher than in the dictator game, implying that proposers are motivated to avoid the potential rejection[17]. Indeed, in the ultimatum game, recipients reject offers below 20% about half the time. Another important element in social interaction is captured by a trust game, in which one of the players (investor) invests a proportion of his or her money. This money then is multiplied, often tripled, and transferred to the other player (trustee). The trustee then decides how much of this transferred money is returned to the investor. The amount of money invested by the investor measures the trust of the investor in the trustee, and the amount of repayment reflects the trustee's trustworthiness. Thus, trust games quantify the moral obligations that a trustee might feel toward the investor. Empirically, investors tend to invest roughly half their money, and trustees tend to repay an amount comparable to the original investment[17].

Studies on experimental games in nonhuman primates can provide important insights into the evolutionary origins of social preference shown by human decision makers. For example, when chimpanzees are tested in a reduced form of the ultimatum game in which proposers choose between two different preset offers, they tend to choose the options that maximize their self-interest, both as proposers and recipients[34]. Therefore, even though chimpanzees and other nonhuman primates show altruistic behaviors, fairness is much more important in social decision making for humans.

Learning in social decision making

When a group plays the same game repeatedly, some players may try to train other players. For example, recipients in an ultimatum game may reject some offers, not as a result of aversion to inequality, but to increase their long-term payoff by penalizing greedy proposers. To better isolate the effect of social preference, therefore, many experimenters do not allow their subjects to interact with the same partners repeatedly. In real situations, however, learning is important, as people and animals do tend to interact with the same individuals repeatedly.

Reinforcement learning theory[2] formalizes the problem faced by a decision maker trying to discover optimal strategies in an unfamiliar environment (**Fig. 2**). This theory has been successfully applied to an environment that includes multiple decision makers[17,20,21,35,36]. The sum of future rewards expected from a particular action in a particular state of the environment is referred to as the value function. Future rewards are often exponentially discounted, so that immediate rewards contribute more to the value function. Similar to utility functions in economics, value functions determine the actions chosen by decision makers. In addition, the difference between the reward predicted from the value function and the actual reward is termed reward prediction error. In simple or direct reinforcement learning algorithms, value functions are updated only for chosen actions and only when there is a reward prediction error[2].

Although reward has a powerful effect on choice behavior, decision makers receive many other signals from their environment. For example, they may discover, after their choices, how much reward they could have received had they chosen a different action. When such

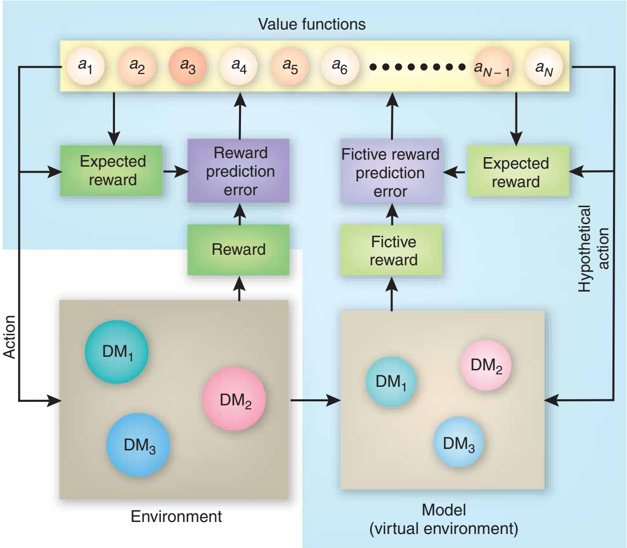


Figure 2 A model-based reinforcement learning model applied to social decision making. The decision maker receives reward according to his or her own action and those of other decision makers (DM) in the environment and updates the value functions according to the reward prediction error. In addition, the decision maker updates his or her model of the environment, including the predicted actions of other decision makers. The fictive reward prediction errors resulting from such model simulations also influence the value functions. The blue background indicates computations internalized in the decision maker's brain.

hypothetical payoffs or fictive rewards differ from the rewards expected from the current value functions, the resultant error signals, called fictive reward prediction error[37] or regret[38], can be used to update the value functions of corresponding actions. Such errors can indeed influence the decision maker's subsequent behaviors during financial decision making[37]. In model-based reinforcement learning algorithms, fictive reward signals can be generated from various types of simulations or inferences based on the decision maker's model or knowledge of the environment. These fictive reward signals might be crucial in social decision making when the simulated environment includes other decision makers (**Fig. 2**).

In game theory, estimating the payoffs from alternative strategies based on the expected actions of other players is referred to as belief learning[16,17]. For example, imagine you observe that a particular decision maker tends to apply the strategy of tit-for-tat during a repeated prisoner's dilemma game. By simulating hypothetical interactions, you can update the value functions for cooperation and defection and might discover that cooperation with this player would produce a higher average payoff than defection. Belief learning and other model-based reinforcement learning algorithms can also update value functions for multiple actions simultaneously. So far, studies on competitive games in humans and other primates have failed to provide strong evidence for such model-based reinforcement learning or belief learning[20,36,39,40]. In contrast, both theoretical and empirical studies show that the reputation and moral characters of individual players influence the likelihood and degree of cooperation[41–43]. For example, a player who has donated frequently in the past is more likely to receive donations when such information is publicly available[42]. Similarly, people tend to invest more money as investors in trust games when they face individuals with positive moral qualities[43]. Therefore, belief learning models might account for how images of individual players are propagated.

Neural basis of reinforcement learning

During the last decade, reinforcement learning theory has become a dominant paradigm for studying the neural basis of decision making (see other articles in this issue and ref. 44). In nonhuman primates, midbrain dopamine neurons encode reward prediction errors[10,45]. Dopamine neurons also decrease their activity when the expected reward is delayed[46] or omitted[10,47]. In addition, neurons in many areas of the primate brain, including the amygdala[48], the basal ganglia[49–51], the posterior parietal cortex[3,52,53], the lateral prefrontal cortex[54–56], the medial frontal cortex[57–59] and the orbitofrontal cortex[60–62], modulate their activity according to rewards and value functions. Nevertheless, how these signals related to value functions in many areas are updated by real and fictive reward error signals and influence action selection is still largely unknown[63].

In human neuroimaging, signals related to expected reward are found in several brain areas, such as the amygdala, the striatum, the insula and the orbitofrontal cortex[64–66]. The noninvasive nature of neuroimaging makes it possible to investigate the neural mechanisms of complex financial and social decision making in humans. On the other hand, the signals measured in neuroimaging studies, such as blood oxygen level–dependent (BOLD) signals, reflect the activity of individual neurons only indirectly. In particular, BOLD signals in functional magnetic resonance imaging (fMRI) experiments may reflect inputs to a given brain area more closely than outputs from it[67]. Comparisons of results obtained from single-neuron recording and fMRI studies must take into consideration such methodological differences.

Neural correlates of social decision making

Socially interactive decision making tends to be dynamic, and the process of discovering an optimal strategy can be further complicated because decision makers often act according to their preferences concerning the consequences to other individuals, often referred to as 'other-regarding preferences'. Nevertheless, the basic neural processes involved in outcome evaluation and reinforcement learning might be generally applicable, whether or not the outcome of choice is determined socially. For example, neurons in the dorsolateral prefrontal cortex of rhesus monkeys often encode signals related to the animal's previous choice and its outcome conjunctively, not only during a memory-saccade task[68] but also in a computer-simulated matching-pennies task[56]. Neurons in the posterior parietal cortex also modulate their activity according to expected reward or its utility during both a foraging task[52] and a computer-simulated competitive game[53]. Similarly, in imaging studies, many brain areas involved in reward evaluation and reinforcement learning, such as the striatum, insula and orbitofrontal cortex, are also recruited during social decision making (**Fig. 3**). However, as described below, activity in these brain areas during social decision making is also influenced by factors that are particular to social interactions.

One of the areas that is critical in socially interactive decision making is the striatum. During decision making without social interaction, activity in the striatum is influenced by both real and fictive reward prediction errors[11,12,37]. Reward prediction errors during social decision making also lead to activity changes in the striatum. For example, during the prisoner's dilemma game, cooperation results in a positive BOLD response in the ventral striatum when cooperation is reciprocated by the partner, but produces a negative BOLD response in the same areas when the cooperation is not reciprocated[69,70]. In addition, the caudate nucleus of the trustee in a repeated trust game shows activity correlated with the reputation of the investor[71]. When investors

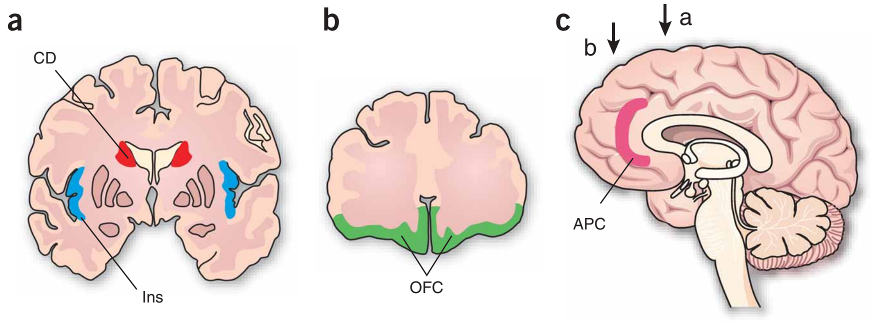


Figure 3 Brain areas involved in social decision making. (**a**,**b**) Coronal sections of the human brain showing the caudate nucleus (CD), the insula (Ins) and the orbitofrontal cortex (OFC). (**c**) Sagittal section showing the anterior paracingulate cortex (APC). Arrows indicate approximate locations of the sections shown in **a** and **b**.

in trust games receive detailed descriptions of the trustees' positive moral characters, the investors tend to invest money more frequently. Moreover, activity in the caudate nucleus of the investor related to the decision of the trustee is attenuated or abolished when the investor relies on information about the trustee's moral character[43].

As described above, theoretical and behavioral studies show that altruistic punishment of unfair behaviors promotes cooperation. Neuroimaging studies provide important insight into the neural mechanisms for producing such costly punishing acts. For example, during the ultimatum game, unfair offers produce stronger activation in the recipient's anterior insula when they are rejected than when they are accepted[72]. Because the insula is involved in evaluation of various negative emotional states, such as disgust[73], its activation during the ultimatum game might reflect negative emotions associated with unfair offers. In addition, the investors who have the option of punishing unfair trustees during the trust game at a cost to themselves often apply such punishment[74]. This punishment may have some hedonic value to the investors, as activity in the caudate nucleus of the investor is correlated with the magnitude of punishment and increases only when punishment is effective. Comparing the proposer's brain activity during the ultimatum game and the dictator game shows that the dorsolateral prefrontal cortex, lateral orbitofrontal cortex and caudate nucleus are important in evaluating the threat of potential punishment[75].

Inequality aversion can give rise not only to altruistic punishment of norm violators but also to charitable donation. The mesolimbic dopamine system, including the ventral tegmental area and the striatum, is activated by both personal monetary reward and the decision to donate money to charity[76]. In contrast, activity in the lateral orbitofrontal cortex increases when decision makers oppose a charitable organization by refusing to donate. Activity in the caudate nucleus and ventral striatum increases with the amount of money donated to a charity, even when the donation is mandatory[77], but the activity in both of these areas is higher when the donation is voluntary.

Although fairness norms strongly influence social decision making, what is considered fair is likely to depend on various contextual factors, such as the sense of entitlement[78] and the need for competitive interactions with other players[79]. Similarly, when two participants play the same game and receive a monetary reward for correct answers, activity in the ventral striatum increases with the amount of money paid to the subject but decreases with the amount of money earned by the partner[80]. In other words, when the subjects are evaluated and rewarded by the same criterion, activity in the ventral striatum is more closely related to the subject's relative payment compared to the partner's payment than to the absolute payment of the subject.

This result raises the possibility that the striatal response to the reward received by others might change depending on whether a particular social interaction is perceived as competition or cooperation. Indeed, during a board game in which the subjects are required to interact competitively or cooperatively, several brain areas are activated differentially depending on the nature of the interaction[81]. For example, compared to competition, cooperation results in stronger activation in the anterior frontal cortex and medial orbitofrontal cortex. However, whether and how these cortical areas influence the striatal activity related to social preference is not known.

Social decision making frequently requires theory of mind—the ability to predict the actions of other players based on their knowledge and intentions[82,83]. Many neuroimaging studies find that social interactions with human players produce stronger activations than similar interactions with computer players in several brain areas[84–86], typically including the anterior paracingulate cortex (**Fig. 3c**). Assuming that more sophisticated inferences are used to deal with human players than with computer players, such findings might provide some clues concerning the cortical areas specialized for theory of mind. Accordingly, the anterior paracingulate cortex might be important in representing mental states of others[82,84–88]. In the trust game, the cingulate cortex seems to represent information about the agent responsible for a particular outcome[89]. The cortical network involved in theory of mind and perception of agency, however, is still not well characterized and is likely to involve additional areas. For example, the posterior superior temporal cortex is implicated in perception of agency[83,86,88], and its activity correlates with the subject's tendency toward altruistic behavior[90].

Genetic and hormonal factors in social decision making

The fitness value of many social behaviors, such as cooperation with genetically unrelated individuals, often depends on various environmental conditions, including the prevalence of individuals with the same behavioral traits. Thus, individual traits related to social decision making could remain heterogeneous in the population because the selective forces favoring different traits could be balanced[91]. Indeed, studies on experimental games commonly show substantial individual variability in the behavior of decision makers, and neuroimaging studies on social behavior find that activity in several brain areas, such as the striatum and insula, correlates with the decision maker's tendency to show altruistic behaviors[69,72,74,75]. Some of this variability might be due to genetic factors. For example, the minimum acceptable offer during an ultimatum game is more similar between monozygotic twins than between dizygotic twins[92].

The genetic mechanisms regulating dopaminergic and serotonergic synaptic transmission might underlie individual differences in behaviors and neural circuits implicated in reinforcement learning and therefore contribute to individual variability in social decision making. Among the genes related to dopamine functions, the dopamine receptor D2 (DRD2) gene has received much attention. For example, DRD2 polymorphisms, such as Taq1A and C957T, influence how efficiently decision makers can modify their choice of behavior according to the negative consequences of their previous actions[93,94]. The Taq1A polymorphism also influences the magnitude of fMRI signals related to negative feedback[93]. In contrast, polymorphism in the dopamine- and cyclic AMP–regulated phosphoprotein of molecular weight

32 kDa (DARPP-32) influences the rate of learning based on positive outcomes, and a valine/methionine polymorphism in catechol-O-methyltransferase (COMT) might influence the ability to adjust choices rapidly on a trial-by-trial basis by modulating dopamine in the prefrontal cortex[56,94]. Variations in the proteins involved in serotonin metabolism, such as the serotonin transporter–linked polymorphism (5-HTTLPR), might also influence social decision making[95,96]. For example, rhesus monkeys carrying only the short variant 5-HTTLPR have less ability to switch in object-discrimination reversal learning and show more aggression than monkeys carrying the long variant[97]. Little is known, however, about the neurophysiological changes associated with genetic variability that might underlie behavioral changes in social decision making. In addition, any effects of genetic variability on such complex behaviors as social decision making are likely to involve interactions among many genes and between genes and the environment[96,98].

Hormones are also known to influence social behavior. For example, high testosterone increases the likelihood that a recipient will reject relatively low offers during the ultimatum game[99], and oxytocin increases the amount of money transferred by the investor during the trust game[100].

Conclusion

Social decision making is one of the most complex animal behaviors. It often requires animals to recognize the intentions of other animals correctly and to adjust behavioral strategies rapidly. In addition, humans can cooperate or compete with one another, and various contextual factors influence the extent to which humans are willing to sacrifice their personal gains to increase or decrease the well-being of others. The neural basis of such complex social decision making can be investigated quantitatively by applying game theory. These studies find that the key brain areas involved in reinforcement learning, such as the striatum and orbitofrontal cortex, also underlie choices made in social settings. Nevertheless, our current knowledge of neural mechanisms for social decision making is still limited. This situation will improve as we come to understand the genetic and neurophysiological basis of information processing in the brain's reward system.

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