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Neural basis of quasi-rational decision making

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Standard economic theories conceive homo economicus as a rational decision maker capable of maximizing utility. In reality, however, people tend to approximate optimal decision-making strategies through a collection of heuristic routines. Some of these routines are driven by emotional processes, and others are adjusted iteratively through experience. In addition, routines specialized for social decision making, such as inference about the mental states of other decision makers, might share their origins and neural mechanisms with the ability to simulate or imagine outcomes expected from alternative actions that an individual can take. A recent surge of collaborations across economics, psychology and neuroscience has provided new insights into how such multiple elements of decision making interact in the brain.

Addresses

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Introduction

Decision-making features prominently in all branches of behavioral and social sciences that seek to identify the basic laws of human behavior and social phenomenon. Although decision making has been studied traditionally in many disciplines, such as economics, behavioral ecology, psychology and neuroscience, there has been relatively little collaboration among them. This is changing rapidly, as reflected in an increasing number of neuroeconomic studies of decision making [1–3].

To a first approximation, humans and animals appear to maximize certain positive outcomes, such as utility or pleasure, and economic theories and artificial intelligence research based on this assumption have been quite successful in accounting for a variety of choice behaviors. However, seemingly rational decisions might often result from boundedly rational (see glossary) or quasi-rational heuristics [4,5], especially in social settings. In addition, whereas theories based on rationality assumptions tend to

provide normative description of choice behaviors, heuristics are often influenced by emotions and dynamics of learning. Accordingly, in this review I first discuss recent findings regarding the neural correlates of utility, and then focus on the neural basis of emotional processes and learning in individual and social decision making.

Neural coding of utilities and value functions

In economics, utility has at least two different meanings [6]. Experienced utility is the subjective pleasure from a particular stimulus or event resulting from a given action. By contrast, decision utility refers to an estimate of experienced utility that can be assessed during the process of decision making, similar to value functions (see glossary) in reinforcement learning [7]. Many studies have examined the neural correlates of experienced or decision utility by examining how neural activity is affected by the intensity of affective stimulus or the amount of monetary reward. These studies have found that signals related to upcoming reward are broadly represented in a network of cortical and subcortical areas, including the striatum [8–11,12*], dorsolateral prefrontal cortex [13], orbitofrontal cortex [14], anterior and posterior cingulate cortex [15,16] and posterior parietal cortex [17]. Most of these areas might be involved in computing or representing decision utility, because they are also activated according to anticipated outcomes when subjects choose among multiple alternatives [18,19**–21**,22*,23*]. Many neurons in these brain regions also code movement parameters, suggesting that competition among different groups of such neurons might provide a mechanism for selecting a particular action based on its decision utility [13,17,18,19**–21*]. Signals related to experienced utility are also found in a distributed network of brain areas, including orbitofrontal cortex [14,24], supplementary eye field [25,26], anterior and posterior cingulate cortex [16,27] and dorsolateral prefrontal cortex (Figure 1; [18]).

The role of emotion in decision making

In the expected utility theory, a decision maker selects an action by maximizing the sum of utilities for various outcomes weighted by their probabilities. Unfortunately, this theory is too simplistic to account for the pattern of choice behavior people display in reality, as illustrated by the Allais' paradox (see Box 1; [28]). Furthermore, economists and psychologists have long recognized that a variety of contextual factors influence the utility of a physical stimulus [29], and that emotions play an important role in decision making [30,31*]. Accordingly, different theories have incorporated these contextual and emotional factors.

2 Cognitive neuroscience

Glossary

Bounded rationality: An assumption that human behavior is only approximately rational as a consequence of limited cognitive capabilities and regularities in the environment.

Counter-factual reasoning: Inference based on simulated or imagined outcomes rather than real outcomes.

Expected utility theory: An economic theory assuming that choice is made to maximize the sum of decision utilities for various outcomes weighted by their probabilities.

Homo economicus (economic man): A rational and self-interested decision maker.

Nash equilibrium: A set of strategies for all players from which no players can increase their payoffs by altering their strategies individually.

Prospect theory: A theory proposed by Daniel Kahneman and Amos Tversky, in which choice outcomes are evaluated relative to a reference point (rather than in absolute terms), and weighted by a non-linear function of probabilities (rather than by probabilities).

Value function: Numerical estimate for the total sum of future rewards expected from a particular action or a particular state of the environment.

Box 1 Allais' paradox

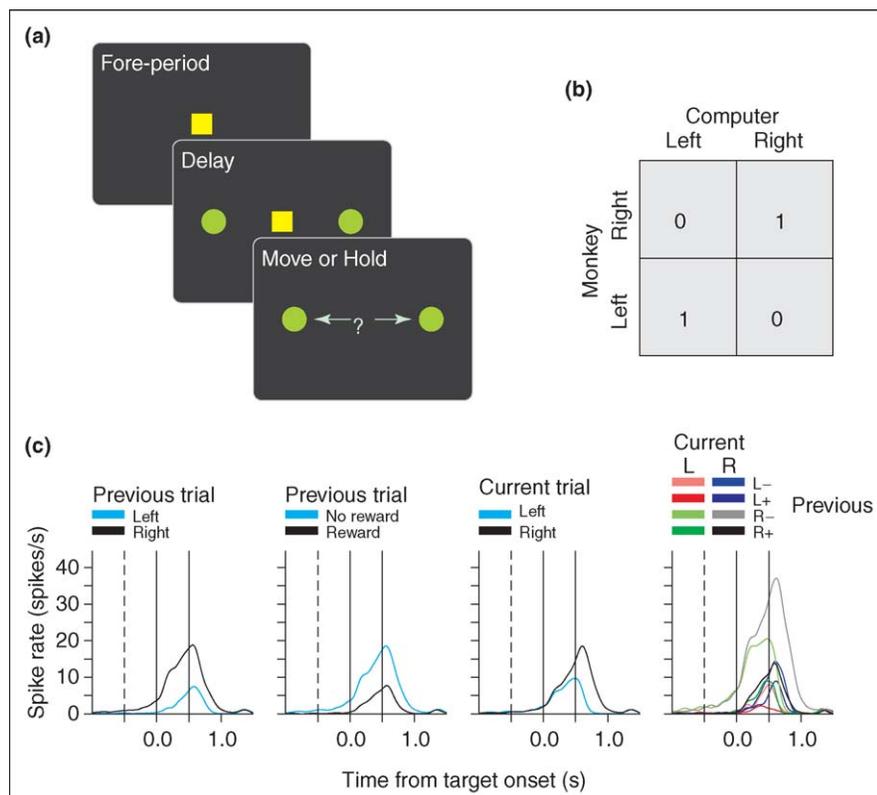
Allais [28] used the following two choice problems to demonstrate a failure of the expected utility theory in predicting the choice behavior of people. A decision maker chooses between the two options A and B in the first problem, and between C and D in the second problem. The values in the table indicate the probabilities for each payoff.

Choice	\$0	Payoff \$1,000	\$5,000
A	0.0	1.0	0.0
B	0.01	0.89	0.1
C	0.89	0.11	0.0
D	0.90	0.0	0.1

Denoting the utility of x as $u(x)$ and assuming $u(\$0)=0$, the expected utility theory proposes that $u(A) = u(\$1,000)$, $u(B) = 0.89 u(\$1,000) + 0.1 u(\$5,000)$, $u(C) = 0.11 u(\$1,000)$, and $u(D) = 0.1 u(\$5,000)$. Accordingly, $u(A) > u(B)$ implies $u(C) > u(D)$. In reality, however, most people prefer A to B and prefer D to C [29].

To account for the Allais' paradox, for example, prospect theory (see glossary) introduces a subjective bias towards certainty through a non-linear transformation of probability [29]. However, there are alternative theories. For

example, regret theory resolves this paradox by postulating that people tend to minimize anticipated regret [32,33]. In this theory, regret is defined as a cognitive or emotional reaction associated with the realization that an unchosen action would have yielded a better outcome

Figure 1

Activity in prefrontal cortex related to the outcomes of previous decisions. **(a)** A free-choice task used by Barraclough *et al.* [18]. In this study, monkeys indicated their choices between two peripheral targets with saccadic eye movements. **(b)** The payoff matrix of a matching pennies game used in the free-choice task. **(c)** Activity of an example neuron in the dorsolateral prefrontal cortex that was modulated by the animal's choice in the previous trial (first column), its outcome (second column), and the animal's choice in the current trial (third column). This neuron was maximally active when the animal selected the right-hand target after receiving no reward for selecting the same target in the previous trial (last column).

than the chosen action. Therefore, regret arises from counter-factual reasoning (see glossary), namely inferences based on hypothetical or imagined outcomes. According to regret theory, people prefer a sure payment of \$1000 in the Allais' paradox because this excludes the possibility of regret that might arise from choosing the alternative lottery and earning nothing. Theories of decision making that are formed on the basis of affective processes, such as regret, have been corroborated by empirical results from behavioral and neurobiological experiments [30,34^{**},35^{**}]. For example, the orbitofrontal cortex might be involved in the process of combining information about the obtained and unobtained outcomes. A lesion in the orbitofrontal cortex impairs the ability to use information about unrealized payoffs to update decision-making strategies appropriately [34^{**}], whereas the difference between the actual and the unobtained outcomes activates a network of cortical areas including the orbitofrontal cortex in addition to the anterior cingulate cortex and anterior hippocampus [35^{**}].

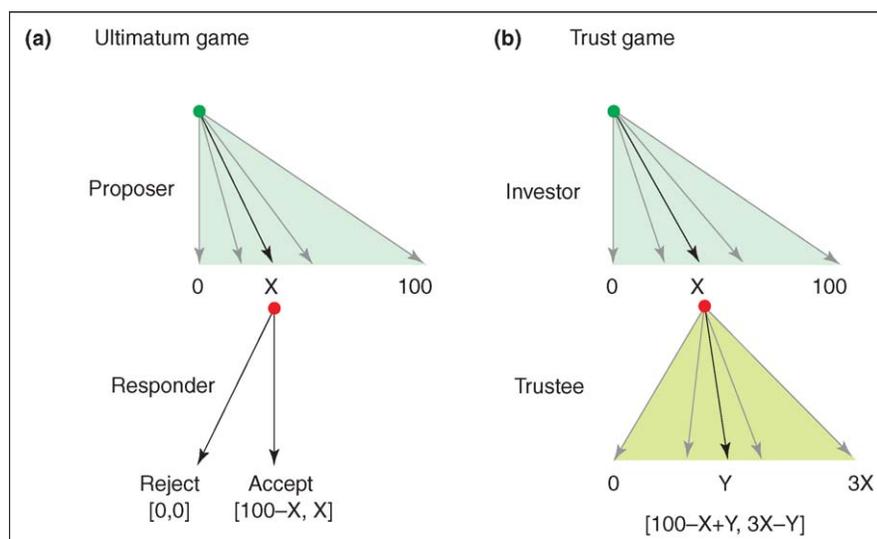
Other emotions, such as elation and disappointment, also arise from counter-factual reasoning when the obtained outcome is better or worse than expected. In contrast to regret, these emotions arise when the outcomes are determined irrespective of the chosen action. Elation and disappointment resemble positive and negative reward prediction errors in reinforcement learning [7], but these emotions can be evoked by a variety of

contextual factors that might not be useful for learning. People commonly express disappointment even when the outcomes of their decisions are determined entirely by chance, and animals react negatively even when they are merely exposed to the possibility of receiving a better outcome [36,37]. Consistent with these behavioral observations, signals related to anticipated rewards seem to be coded in relative terms, as demonstrated in ventral and dorsal striatum [38], sublentiform extended amygdala [39], orbitofrontal cortex [40], dorsolateral prefrontal cortex [41] and posterior parietal cortex [20^{**}]. According to prospect theory, the outcome of a decision is evaluated relative to a reference point, such as the status quo [29]. Therefore, relative coding of reward signals is consistent with prospect theory. Relative values of rewards might be computed in a particular brain region and broadcast to other areas, but the mechanisms for such computation are poorly understood and should be explored in future studies.

Social decision making

The nature of decision-making changes fundamentally when individuals begin to interact in a social setting, making the outcome of a decision also dependent on the decisions of others. Many aspects of social cognition and related emotional processes are now being probed by neurobiological investigations. In particular, neurobiological studies utilizing game theoretic tasks have provided some important results (Figures 1 and 2). Game theory characterizes the problem of social interaction with a

Figure 2



Examples of an ultimatum game (a) and a trust game (b). **(a)** Ultimatum game. The proposer divides a given sum of money (\$100 in this example) by offering $\$X$ to the responder. The responder then either rejects the offer, leaving nothing for either player, or accepts the offer. The Nash equilibrium for this game is for the proposer to offer as little as possible and for the responder to accept any offer. In reality, the proposer often offers a substantial amount of money and unfair offers are often rejected. **(b)** Trust game. The investor divides a sum of money (\$100) by investing $\$X$ to the trustee. The invested money is immediately tripled. The trustee then returns a portion of this money ($\$Y$) to the investor and keeps the remaining amount. The Nash equilibrium is for the trustee to invest nothing and for the trustee to return nothing, but this rarely happens [43]. The first and second numbers inside the brackets at the bottom of the figure show the payoffs to the first (proposer or investor) and second (responder or trustee) players, respectively.

Box 2 Nash equilibria in simple games

Game theory provides a useful tool to study the neural basis of decision making, because they often produce a rich pattern of choice behavior with a relatively simple set of rules. Some games used in recent neuroeconomic studies and their Nash equilibria are described below.

Matching pennies: Each player chooses between two alternatives (e.g., head or tail of a coin). One player (matcher) wins if the two choices are the same, and the other (non-matcher) wins otherwise. If the payoffs for the two choices are identical, Nash equilibrium for this game is to select the two alternatives randomly with equal probabilities.

Prisoner's dilemma: In this game, each player can defect (D) or cooperate (C). The payoffs from D and C for a given player are p and q when the other player chooses D, and r and s if the other player chooses C, and $r > s > p > q$. Thus, the Nash equilibrium is mutual defection, but this is worse (p) for both players than mutual cooperation (s).

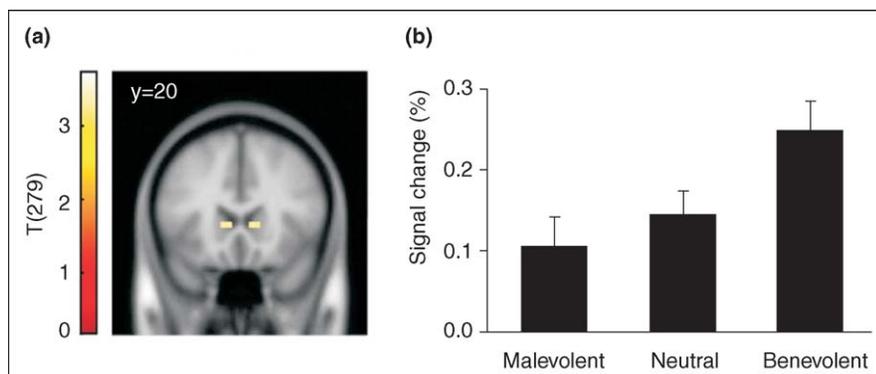
Trust game: An investor sends part of a fixed amount of money to the trustee, and this investment is multiplied by a factor. The trustee then returns some money to the investor. The Nash equilibrium is to exchange no money (Figure 2).

Ultimatum game: A proposer offers part of a fixed amount of money to a responder, who then either accepts or rejects the offer. The Nash equilibrium is for the proposer to offer as little as possible, and for the responder to accept any offer (Figure 2).

payoff matrix for multiple decision makers (players) and a set of alternative actions available to each player (see Box 2). Classical game theory predicts that a group of self-interested players would reach a set of strategies, known as Nash equilibrium [42], from which no players can increase their payoffs individually. Similar to the experimental studies on expected utility theory, however, empirical studies have frequently demonstrated that people seldom play according to such equilibrium strategies [43]. Accordingly, behavioral and neurobiological studies of social decision making are likely to elucidate the nature of such discrepancies.

It has been found in several imaging studies that the brain areas involved in processing reward signals during individual decision-making also play important roles during experimental games and other types of social interactions. Furthermore, changes in the intensity or timing of these signals might provide important clues as to how these brain regions function during social decision-making. For example, the caudate nucleus changes its activation according to the reward prediction error in stochastic decision-making tasks [22*,23*], but alters the timing of its activation according to the expectation of benevolent reciprocity during a trust game (Figures 2b and 3; Box 2; [44**]). Activity in some cortical areas is often enhanced during interactions with human partners compared with activity during similar interactions with computer partners [45–47,48**], suggesting that decisions made during social interactions might be influenced by factors not directly related to payoffs. For example, during an ultimatum game, a proposer divides a particular amount of money and offers part of it to a responder (Figure 2a, Box 2). Contrary to the prediction of Nash equilibrium, small offers are often rejected, and such unfair offers activate the anterior insula more strongly when the players interact with other human players than with computers [46]. Similarly, anterior cingulate cortex and striatum are activated during mutual cooperation in the prisoner's dilemma only when subjects believe that they are interacting with people rather than a computer opponent [47].

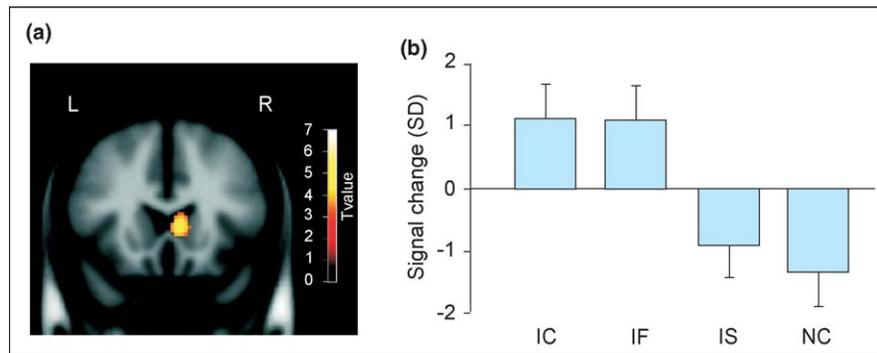
Activity that is evoked by interaction with human partners in the brain areas that ordinarily display signals related to anticipated reward might reflect a neurobiological mechanism to facilitate cooperation. For example, the caudate nucleus is activated when humans desire to punish their uncooperative partner in economic exchange (Figure 4; [49**]). Given the importance of cooperation in social behaviours [50], cooperation and other altruistic

Figure 3

Activation in the striatum during a trust game. (a) King-Casas *et al.* [44**] found that during a trust game there was greater activation in the trustee's caudate nucleus when the investor's benevolent decision was revealed compared with that in response to a malevolent decision.

(b) Activation in the trustee's caudate nucleus changed systematically depending on whether the investor's response was malevolent, neutral or benevolent.

Figure 4



Activation in the striatum related to altruistic punishment. (a) de Quervain *et al.* [49**] found activation in the caudate nucleus associated with a desire to punish others. (b) Magnitude of activation in the caudate nucleus changed with the nature of punishment. It was greater when the subject made the decision to punish and this punishment was costly (IC) or when the punishment was intentional but not costly (IF), compared with when the subject sent a symbolic message instead of real punishment (IS), or when the trustee's decision was determined randomly and the punishment was costly (NC).

behaviors might be controlled by multiple mechanisms. For example, inhalation of oxytocin during a trust game increases the amount paid by the investor to the trustee, suggesting that hormonal factors might also contribute to cooperation [51**].

Learning and decision making

Decision and experienced utilities, or anticipated and actual outcomes, might not always coincide, especially in a dynamic environment. In addition, utilities must be calibrated when the environment changes, for example when you try to find a favorite restaurant in a new city. In reinforcement learning, discrepancy between predicted and actual rewards is referred to as reward prediction error, and used to update decision utilities or value functions [7]. Reward prediction errors are encoded by the dopamine neurons in the ventral tegmental area and substantia nigra [52*,53*,54,55]. Dopamine inputs carrying reward prediction errors and cortical inputs carrying signals related to the behavioral outputs converge in the striatum. This potentially provides an anatomical substrate for updating value functions and utilities [22*,23*].

Reinforcement learning algorithms and related neural machineries might be applicable to decision-making problems in complex social settings. Although game theory provides normative solutions, such as the Nash equilibrium (see glossary), people often deviate systematically from such solutions even in relatively simple games, and successful strategies are learned through experience [43,56]. In reinforcement learning, strategies are improved by updating value functions according to the actual payoffs received at the end of each play. This successfully accounts for the behaviors of people and animals in relatively simple games, such as matching pennies [57,58]. For more complex games, however, reinforcement learning is not very efficient, because it

ignores potentially valuable information about the strategies of other players. By contrast, belief learning theory assumes that players update their beliefs about the behaviors of other players, and choose their actions by maximizing the expected payoff given such beliefs [43,56].

When a player's belief about the strategies of other players is updated, this can alter the payoffs expected from all actions. For example, during the rock-paper-scissors game, the payoff expected from each action would change according to the expected behavior of the opponent. Computationally, therefore, belief learning requires a player to update value functions for all possible actions indiscriminately according to the actual payoffs received and the hypothetical payoff that would have resulted if an alternative action had been chosen. Empirical evidence for belief learning is mixed [58–61]. However, hybrid models in which value functions are adjusted by the actual and hypothetical payoffs to different degrees tend to account for the empirical data better than simple reinforcement learning models do in both humans and monkeys [61,62]. Thus, inferences based on hypothetical payoffs might contribute to optimizing the process of decision-making during social interaction. However, the neural mechanisms for revising decision utilities according to hypothetical payoffs during social interaction is little understood (but see [63**]).

Mentalizing and theory of mind

When the same game is played repeatedly, decision makers can accumulate information about the behaviors of other players and adjust their decision-making strategies accordingly. Because the expected payoffs can be uniquely determined by a particular combination of choices made by the other players, a decision maker might choose to make direct modifications in value functions of alternative actions after each play. Alternatively,

this might be accomplished by updating the player's internal models about the strategies of other players. The ability to represent the mental states of others, such as their beliefs, desires and knowledge, is referred to as theory of mind, and this might provide a more parsimonious description for the behaviors of other members in a group. Theory of mind, therefore, might play a key role in optimizing decision-making strategies during social interactions. This ability might be unique to humans [64], although a more primitive form might be found in non-human primates, especially when they are engaged in competitive interactions [65,66].

Investigation of neural processes involved in socially interactive decision-making might provide some clues as to how such capabilities have evolved. For example, anterior paracingulate cortex is activated in various tasks designed to characterize theory of mind [63^{**},67,68]. Interestingly, this area is also activated during experimental games, but more strongly when the subjects believe that they are interacting with real human partners instead of a computer opponent [44^{**},47,69]. These results suggest that an important function of the anterior paracingulate cortex might be to decouple information obtained from simulations and inferences about the mental states of other individuals from reality [67,68]. Nevertheless, theory of mind and other aspects of social cognition are likely to engage multiple cortical systems, including the temporo-parietal junction area [70], and exactly how they are coordinated during social reasoning needs to be understood better (see Saxe's article in this issue). In addition, whether and how the process of social reasoning is implemented in the brains of non-human primates need to be examined in future studies.

Conclusions

Formal theories formed on the basis of the assumptions of rationality might not account for the rich pattern of real-life decisions, but they can still provide valuable tools to analyze complex decision-making problems and generate hypotheses about the corresponding cognitive and neural processes. Efforts to narrow the gap between such formal theories and real choice behaviors are also manifest in studies of emotion-based choices and learning in decision making. Neurobiological studies of decision-making benefit greatly from such theoretical and behavioral studies. These collaborations will ultimately enable us to understand how we decide what we want to do.

Update

A recent study examined the neural activity in the striatum of monkeys performing a stochastic decision-making task, and experimenters found that many neurons encoded the value of a specific action rather than the action itself [71]. Singer *et al.* found that empathy-related activations in the insular and anterior cingulate cortices were reduced when the subjects observed unfair players,

namely those who behaved unfairly in an economic game, be subjected to pain [72]. This study provides additional evidence that cooperation is facilitated by multiple neural mechanisms.

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by the other player. Activation in the trustee's caudate nucleus was related to the benevolent reciprocity of the investor, and provided the 'intention to trust' signal. Initially, this activation began after the investor's decision was revealed, but eventually occurred before the investor's decision, suggesting that the trustee gradually developed a model for the investor's behavior.

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