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problem-solving. However, we suggest that the FPC function is restricted to the processing of simple cognitive branching, whereby only a single task can be maintained in a pending state at any one time. This hypothesis places severe serial and recursive constraints on human reasoning, problem-solving, and complex decision-making. Consistent with this view, it appears unlikely that the human brain has evolved to solve complex problems such as deciding the next move in a game of chess. Selective pressure to survive in a physically challenging environment may place other demands before the need for such higher cognitive faculties. Nevertheless, a capacity-limited FPC function may have endowed humans with two key adaptive advantages: on the one hand, an ability to pursue long-term behavioral plans and at the same time respond to demands of the physical or social environments; on the other hand, to explore any potential gain from the interposition of new task sets within ongoing behavioral routines or from the contingent recombination of previously established behavioral plans, as in genetic recombination mechanisms. Thus, the frontopolar cortex may have played an even more critical role in the gradual formation of complex behavioral and cognitive routines such as tool use in individuals and societies, that is, in human creativity rather than complex decision-making and reasoning.

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36. This work was supported by a European Young Investigator award to E.K.

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10.1126/science.1142995

REVIEW

Social Decision-Making: Insights from Game Theory and Neuroscience

Alan G. Sanfey

By combining the models and tasks of Game Theory with modern psychological and neuroscientific methods, the neuroeconomic approach to the study of social decision-making has the potential to extend our knowledge of brain mechanisms involved in social decisions and to advance theoretical models of how we make decisions in a rich, interactive environment. Research has already begun to illustrate how social exchange can act directly on the brain's reward system, how affective factors play an important role in bargaining and competitive games, and how the ability to assess another's intentions is related to strategic play. These findings provide a fruitful starting point for improved models of social decision-making, informed by the formal mathematical approach of economics and constrained by known neural mechanisms.

Our lives consist of a constant stream of decisions and choices, from the everyday (will I respond to this e-mail?) to the highly consequential (will I have a child?). Essentially, the study of decision-making attempts to understand our fundamental ability to process

multiple alternatives and to choose an optimal course of action, an ability that has been studied by various disciplines with different theoretical assumptions and measurement techniques, although with relatively little integration of findings.

The emergence of an interdisciplinary field, popularly known as neuroeconomics (1, 2), has begun to redress this lack of integration and offers a promising avenue to examine decision-making at different levels of analysis. Its propo-

nents seek to better understand decision-making by taking into account cognitive and neural constraints, as investigated by psychology and neuroscience, while using the mathematical decision models and tasks that have emerged from economics.

Most experimental studies of decision-making to date have examined choices with clearly defined probabilities and outcomes, such as choosing between monetary gambles. Given that we live in highly complex social environments, however, many of our most important decisions are made in the context of social interactions, which are additionally dependent on the concomitant choices of others—for example, when we are deciding whether to ask someone on a date or entering a business negotiation. Although relatively understudied, these social situations offer a useful window into more complex forms of decisions, which may better approximate many of our real-life choices.

As part of the neuroeconomic approach, researchers have begun to investigate the psychological and neural correlates of social decisions using tasks derived from a branch of experimental economics known as Game Theory. These tasks, though beguilingly simple, require sophisticated reasoning about the motivations of other players. Recent research has combined these paradigms with a variety of neuroscientific

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methods in an effort to gain a more detailed picture of social decision-making. The benefits of this approach are twofold. First, neuroscience can describe important biological constraints on the processes involved, and indeed, research is revealing that many of the processes underlying complex decision-making may overlap with more fundamental brain mechanisms. Second, actual decision behavior in these tasks often does not conform to the predictions of Game Theory, and therefore, more precise characterizations of behavior will be important in adapting these models to better fit how decisions are actually made.

Game Theory

Game Theory (3) is a collection of rigorous models attempting to understand and explain situations in which decision-makers must interact with one another. It offers a rich source of both behavioral tasks and data, in addition to well-specified models for the investigation of social exchange.

A common criticism of economic models is that observed decision behavior typically deviates, often quite substantially, from the models' predictions. Most classical game theoretical analyses predict that rational, self-interested players will make decisions to reach outcomes, known as Nash equilibria (4), from which no player can increase his or her own payoff unilaterally. However, players rarely play according to these strategies [see (5) for a useful summary of the primary findings in this field]. In reality, decision-makers are generally less selfish and strategic than the model predicts and value social factors such as reciprocity and equity. Nonetheless, the well-characterized tasks and formal modeling approach offered by Game Theory provides a useful foundation for the study of decisions in a social context. Although the rules of these games are typically simple, these tasks produce a surprisingly varied and rich pattern of decision-making.

One focus of Game Theory is strategic bargaining behavior; the Ultimatum Game (UG) (6) is often used to examine responses to fairness. In the UG, two players must divide a sum of money, with the proposer specifying this division. The responder has the option of accepting or rejecting the offer. If the offer is accepted, the sum is divided as proposed. If it is rejected, neither player receives anything. If people are motivated purely by self-interest, the responder should accept any offer and, knowing this, the proposer will offer the smallest nonzero amount. However, this Nash equilibrium prediction is at

odds with observed behavior, and the modal offer is a 50/50 split. Further, low offers of less than 20% of the total amount are rejected about half of the time (6). Thus, people's choices in the UG do not conform to a model in which decisions are driven by financial self-interest, and neuroscience has begun to offer clues as to the mechanisms underlying these decisions.

Reciprocal exchange has also been studied extensively in the laboratory, exemplified by the Trust Game (TG) and the Prisoner's Dilemma. In the first (7), a player (the investor) must decide how much of an endowment to invest with a partner (the trustee). Once transferred, this money is multiplied by some factor, and then the trustee has the opportunity to return money to the investor, but, it is important to note, need not return anything. If the trustee honors trust and returns money, both players end up with a higher monetary payoff than the original endowment. However, if the trustee abuses trust and keeps the

each. The Nash equilibrium for the PDG is mutual defection, a worse outcome for both players than mutual cooperation, but again, in most iterations of the game, players exhibit more trust than expected, with mutual cooperation occurring about 50% of the time.

Finally, coordination games (9) offer insights into how we assess the preferences of others and choose accordingly. For example, in matching pennies, players choose between two alternatives (heads or tails). One player wins if the two choices are the same, and the other wins if they are different. Players typically approach this game by attempting to infer the strategy of the opponent, thus providing a window into how we use intention-detection processes to assist our strategic decision-making.

Current Research Directions

Researchers have sought to investigate brain function in human subjects as they interact with other people in real, consequential social scenarios (e.g., by playing bargaining, reciprocal exchange, and coordination games with partners). Although this approach is a relatively recent endeavor, several interesting themes have emerged in current research: (i) social reward; (ii) competition, cooperation, and coordination; and (iii) strategic reasoning.

Social reward. Neuroeconomic research tries to illuminate the process by which we encode decision outcomes and how this might, in turn, guide our future choices. It is widely hypothesized that the brain uses a common-reward metric, which is crucial for a system to choose

between rewards delivered in different modalities. A strong candidate for this metric is the mesolimbic dopamine system, and single-cell recordings from neurons in the striatum, a major projection site of midbrain dopamine cells (see Fig. 1), have shown that neural responses scale reliably with reward magnitude (10). These results also are observed in humans, with activity changes in the striatum scaling directly with the magnitude of monetary reward or punishment (11, 12). In simple coordination games, researchers have uncovered compelling evidence for the existence of reinforcement-learning mechanisms in nonhuman primates (13, 14). This mechanism is thought to improve choices over time, by continually updating the outcomes according to the rewards and punishments encountered in the environment.

Building from this basic research, researchers have discovered that the human striatum appears to be centrally involved in social decisions, above and beyond any financial outcome that may

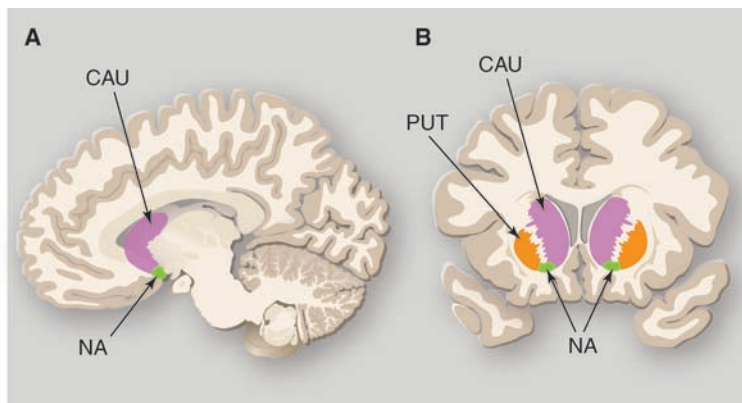


Fig. 1. The subcomponents of the striatum, involved in the processing of reward. (A) Sagittal section and (B) coronal section illustrate the location of the caudate nucleus (CAU), putamen (PUT), and nucleus accumbens (NA).

entire amount, the investor takes a loss. As the investor and trustee interact only once during the game, Game Theory predicts that a rational and selfish trustee will never honor the trust given by the investor. The investor, realizing this, should never place trust in the first place, and so will invest zero in the transaction. Despite these grim theoretical predictions, a majority of investors do in fact send some amount of money to the trustee, and this trust is generally reciprocated.

The standard Prisoner's Dilemma game (PDG) (8) is similar, except that both players simultaneously choose whether or not to trust each other, without knowledge of their partner's choice. In the PDG, payoffs depend on the interaction of the two choices. The largest payoff to the player occurs when he or she defects and the partner cooperates, with the worst outcome when the decisions are reversed (player cooperates while partner defects). Mutual cooperation yields a modest payoff to both players, whereas mutual defection provides a lesser amount to

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accrue to the player. Several neuroimaging studies have demonstrated that the striatum tracks a social partner's decision to reciprocate or not reciprocate cooperation, appearing to encode abstract rewards such as the positive feeling garnered by mutual cooperation. Reciprocated cooperation with another human leads to increased activation in the striatum as compared with a control condition where an identical amount of money is earned, whereas unreciprocated cooperation shows a corresponding decrease in activation in this area (15). In addition, activation is associated with increased cooperation in subsequent rounds, which suggests that the striatum may register social prediction errors to guide decisions about reciprocity.

Related findings have been reported in a multiround TG (16), where activation in the trustee's caudate was related to how much reciprocity the investor had shown on previous trials, and thus corresponded to an "intention to trust" signal of the trustee. Further, this signal gradually shifted in time—in early trials the signal occurred after the investor made his or her choice, whereas later on, this signal occurred much earlier, before the investor's decision was revealed. This temporal shift is also reminiscent of reward prediction errors in reinforcement learning models (17).

These prediction error signals from partner decisions can be greatly reduced when decisions are based on prior information. Providing general personality profiles of partners before they play a TG led to reduced caudate activity when responding to partners described in either positive or negative moral terms, although responses to morally neutral players remained unchanged (18). This suggests that prior beliefs can reduce the amount of trial-by-trial learning, which demonstrates both top-down and bottom-up influences on the neural basis of social cooperation.

Of course, social reward need not always be related to positive, mutually cooperative, actions. Players also may derive satisfaction from punishing defectors, even when this punishment leads to a financial loss to the player. This was illustrated in a positron emission tomography study (19) where investors were confronted with non-reciprocators in a TG. Players had the option to punish these defectors, though this also entailed a loss of points for themselves. Nonetheless, players made the decision to punish, and this was associated with activation in the caudate, with activation greater when the punishment was real (involving a financial loss to the defector) than when it was merely symbolic.

Finally, two recent studies have examined the neural basis of social altruism in tasks where players must decide whether to donate money to charitable organizations. In one study (20), the striatum was engaged by both receiving money and by donations to charity. In another (21), these areas were also activated by receipt of money and by observing a donation to a charity, but this activation was enhanced when this charitable donation was voluntary as opposed to forced. The latter studies are intriguing and offer the possibility of extending investigations of social reward beyond simple two-player interactions to interactive decision-making at a societal level, which has potential implications to inform questions of public policy.

Competition, cooperation, and coordination. In addition to the rewarding or punishing effects of social interactions, these scenarios have also illustrated the prominent role emotions play in social decision-making. Classical models of decision-making have largely ignored the influence of emotions on how decisions are made, but recent research has begun to demonstrate the powerful effect these factors play.

Emotional processes seem to reliably engage a set of structures including reward-processing

mechanisms discussed above and areas of the midbrain and cortex to which they project, such as ventromedial prefrontal cortex (VMPFC), orbitofrontal cortex, and anterior cingulate cortex, as well as other areas such as the amygdala and insula (22) (see Fig. 2). Early pioneering work in this domain showed that patients suffering damage to VMPFC who presented with associated emotional deficits were impaired in performing gambling tasks (23), which demonstrated experimentally that emotion plays a vital role in determining decisions.

In terms of social decision-making, negative emotional states are observed behaviorally as a result of both inequity and nonreciprocity, such as unfair offers in a UG (24). These emotional reactions have been proposed as a mechanism by which inequity is avoided and may have evolved precisely to foster mutual reciprocity, to make reputation important, and to encourage punishment of those seeking to take advantage of others (25). Indeed, even capuchin monkeys respond negatively to unequal distributions of rewards by refusing to participate in a task that requires effort if they witness another monkey receiving equal reward for less work (26).

Neuroscientific studies offer the potential to go beyond speculation to examine the causal relationship between an emotional reaction and subsequent social decision, as well as to investigate whether areas specialized for the processing of basic emotions may be co-opted for more complex affective reactions. A functional magnetic resonance imaging study (27) examined unfair behavior in the UG and found brain areas, primarily the anterior insula, that exhibited greater activation as the unfairness (i.e., inequity) of the offer increased. Further, this area was more active when the subject was playing with another human than when engaged with a computer partner. It is noteworthy that the activation of this area predicted the player's decision to either

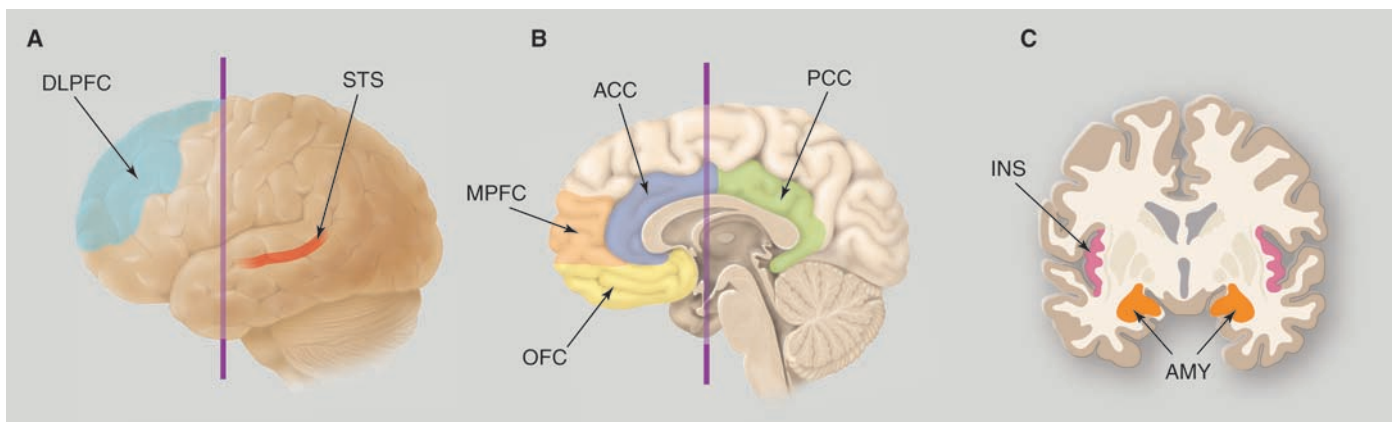


Fig. 2. Map of brain areas commonly activated in social decision-making studies. (A) The lateral view shows the location of the dorsolateral prefrontal cortex (DLPFC) and superior temporal sulcus (STS). (B) The sagittal section shows the location of the anterior cingulate cortex (ACC),

medial prefrontal cortex (MPFC), orbitofrontal cortex (OFC), and posterior cingulate cortex (PCC). (C) The coronal section [cut along the purple line in (B)] shows the location of the insula (INS) and amygdala (AMY). Areas circled are those often associated with ToM processes.

accept or reject the offer, with rejections associated with significantly higher activation than acceptances. In a related study, this area was also active in an iterated PDG (28), where individuals with a stronger anterior insula response to unreciprocated cooperation showed a higher frequency of defection. Finally, the same region has been found in relation to empathic responses when witnessing a fair PDG partner's receiving painful electric shocks (29).

The presence of anterior insula activations in these studies is particularly interesting as this brain region is also responsive to physically painful (30) and disgusting (31) stimuli and is involved in mapping physiological states of the body, including visceral sensations of autonomic arousal (32). Anterior insula and associated emotion-processing areas may play a role in marking a social interaction as aversive and, thus, discouraging trust of that partner in the future.

Separate measures of emotional arousal provide support for this hypothesis. An UG study measuring skin-conductance responses, used as an autonomic index of affective state, found higher skin conductance activity for unfair offers, and as with insular activation, this measure discriminated between acceptances and rejections of these offers (33). Finally, both VMPFC patients (34) and normal players primed with negative emotional states (35) reject unfair offers more frequently than controls in both cases, further evidence that regulation of affective processing is important in social decision-making.

In a similar vein to the suppression of striatal activation by frontal, "top-down" processes in reward studies, activation of frontal regions to unfair offers in UG studies has been interpreted as a mechanism by which other more deliberative goals (such as reputation maintenance or the desire to make money) can be implemented. Transcranial magnetic stimulation was used to disrupt processing in dorsolateral prefrontal cortex while players were making decisions about offers in an UG (36, 37). In both studies, stimulation increased acceptance rates of unfair offers as compared with control situations, which provides strong evidence for a causal relation between activation in this area and social decisions.

A final potentially fruitful avenue of research in cooperative and competitive games is in using neuropeptides such as oxytocin, which is known to facilitate social affiliation in nonhuman animals, to modulate human social relationships. In a TG (38), intranasal administration of oxytocin led to an increase in trust placed by investors. This effect was not general for all types of decisions and was not observed for risk or in games with random outcomes, but rather was specific for consequential social interactions with other humans.

Although this research has greatly increased our understanding of the neural correlates of

social decisions, it also has the potential to inform economic theories. Recent models in behavioral economics have attempted to account for social factors, such as inequity aversion, by adding social utility functions to the standard models [e.g., refs. (39, 40)]. Modeling these functions based on the underlying neural patterns provides a useful constraint in the development of new models.

Strategic reasoning: Theory of mind. An ancillary benefit of these social decision-making tasks is that they can offer insight into how we process the intentions and actions of others, an ability often termed Theory of Mind (ToM). Studies of ToM reveal a network of areas that appear to be involved in this ability, primarily medial prefrontal cortex and anterior paracingulate cortex (41, 42), and decision-making studies have similarly demonstrated activation in these regions when players are immersed in thinking and acting on the beliefs of others, either by guessing partner strategies (43) or when comparing play with another human to play with a random device, such as a computer partner (44, 45). This suggests that these regions may be involved in "intention detection," that is, assessing the meaning of behavior from another agent.

Clearly, other areas may be involved in these ToM processes, such as the tempo-parietal junction (46), and it is also intriguing that these proposed areas largely overlap with those of the brain's purported "default network" (47). Although this integration is not well understood at present, use of social decision tasks offers potentially interesting avenues to uncover exactly how and where we process the meaning behind actions. For example, a recent study (48) uncovered neural activation arranged spatially along the anterior cingulate cortex corresponding to either "me" or "not me" responses in a Trust Game. These activations were only observed in the presence of a partner, which suggests that they were involved in encoding the social aspects of the exchange.

Additionally, some individuals with psychiatric disorders such as autism spectrum disorder have demonstrated severe ToM deficits. Autistic participants had a more difficult time shifting strategy in PDG and also were more likely to accept initial low UG offers (49), which demonstrated shortfalls in the ability to reason successfully in real social interactions.

Conclusion

The preceding sections review some general ways in which experimental economics and neuroscience can be combined to make important new contributions to understanding social decision-making. These findings provide some traction for measuring physical mechanisms responsible for social decision-making and offer the promise of identifying and precisely characterizing both the mechanisms and the factors that

influence their engagement and interaction. Games offer some real advantages over standard decision-making paradigms, not least in their embedding in actual, consequential, social interactions that allow investigation of complex processes such as reputation, trust, equality, and cooperation.

As with any novel approach, there are challenges to address. The component disciplines operate at different levels of analysis and have different theoretical assumptions. More practically, there are important differences in methodology, in particular, with regard to the use of deception, generally prohibited by economics but used extensively in psychology and neuroscience. In addition, it is important to use caution in interpreting neural activations as measured by neuroimaging. For example, the association of a brain region with either value encoding or aversive processing in previous studies does not necessarily mean that activation in this area in the context of an interactive game can automatically be interpreted as rewarding or punishing, respectively. It would therefore be prudent for the field, as a whole, to buttress these claims by either converging evidence from other methodologies or, at the very least, demonstrating behavioral performance in line with the neural predictions, such as a player's preference for options that activate reward centers more strongly (19).

The neuroeconomics of individual decision-making has had some notable success in investigating how parameters of decision utility are represented in the brain (50–52). In a similar vein, the neuroeconomics of social decision-making could probe whether there are neural correlates of parameters that Game Theory both predicts (such as knowledge of payoffs and long-term strategic thinking) and does not predict (such as affective biases and individual differences in ToM ability). In addition, data generated by this approach can prove valuable in providing additional constraints, based on the neural substrate, for any theory that seeks to accurately model social decision-making.

Finally, the neuroscientific endeavor could also profit from allying more closely with the formal models of Game Theory, as opposed to merely viewing it as a useful source of tasks. For example, modeling of behavior in these tasks (53) can yield useful insights as to the decision-making behavior of organisms over time and could help illuminate processes that different games may have in common.

It would also be useful to explore ways in which the various economic approaches may make contact with more traditional neuroscientific frameworks, such as the reinforcement learning models mentioned above. Do the computations described by these models map onto the formal Game Theory analysis?

The ability to better understand how our decisions will affect others—and their decisions

affect us—has relevance from the broadest levels of public policy to our most immediate interpersonal interactions. There is little doubt that the combination of Game Theory tasks, with their formal, detailed mathematical models, and the techniques of modern neuroscience offers fruitful opportunities for the study of social decision-making. This approach can both advance the predictive accuracy of theoretical models by constraining them based on behavioral performance and the underlying neurobiology, as well as further our knowledge of how people make decisions in a social context.

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- The author thanks D. Sbarra, A. Scheres, M. van 't Wout, and two anonymous reviewers for their helpful comments, and L. Chang for assistance with figure design.

10.1126/science.1142996

REVIEW

Decision-Making Dysfunctions in Psychiatry—Altered Homeostatic Processing?

Martin P. Paulus

Decision-making consists of selecting an action from a set of available options. This results in an outcome that changes the state of the decision-maker. Therefore, decision-making is part of a homeostatic process. Individuals with psychiatric disorders show altered decision-making. They select options that are either non-optimal or nonhomeostatic. These dysfunctional patterns of decision-making in individuals with psychiatric disorders may fundamentally relate to problems with homeostatic regulation. These may manifest themselves in (i) how the length of time between decisions and their outcomes influences subsequent decision-making, (ii) how gain and loss feedback are integrated to determine the optimal decision, (iii) how individuals adapt their decision strategies to match the specific context, or (iv) how seemingly maladaptive responses result from an attempt to establish an unstable homeostatic balance.

Before considering what goes wrong with decision-making in psychiatric patients, it is useful to summarize some of the basic conceptualizations and findings regarding decision-making in general. Generically, decision-making is selecting an action from a set of available options, which may result in an outcome that

leads to a different psychological and physiological state of the decision-maker. Decision-making consists of a complex set of processes that are orchestrated in various brain systems to find an optimal outcome. Optimal decision-making requires a set of higher-order cognitive functions by which individuals regulate their

actions, thoughts, and emotions according to current psychological or physiological states, goals, and environmental conditions. In particular, individuals must be able to appraise the momentary status of their needs. Therefore, decision-making is part of a homeostatic process. Homeostasis can be defined as a dynamic physiological, cognitive, and affective steady state (*I*) that integrates multiple bottom-up sensory afferents and top-down cognitive and affective control processes, resulting in dynamic stability (i.e., resistance to internal and external perturbations). Decisions maintain or bring individuals into a new homeostatic state. Temporally, decision-making can be divided into three stages (2): (i) the assessment and formation of preferences among possible options, (ii) the selection and execution of an action (and the inhibition of alternative actions), and (iii) the experience or evaluation of an outcome. Initially, a value or utility is assigned to each available option (3), which determines the preference structure of the decision-making situation. The brain must evaluate not only what is occurring now but also what may or may not

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