

Cooperation in the brain: neuroscientific contributions to theory and policy

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An intriguing feature of human social interaction is the degree to which we are willing to cooperate with others, even when this cooperation is risky and can make us vulnerable. Recent advances in neuroscientific research have begun to provide additional insights into the neural mechanisms of cooperation that can help to better understand the psychological processes that underlie cooperative behavior. In turn, these models of cooperative decision-making can play a valuable role in informing and developing policy interventions aimed at improving societal level cooperation. Here, we outline several lines of current research that are proving useful in understanding the nature of cooperative decision-making, and outline how these research themes can provide promising insights for the development of more effective policy campaigns.

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Interestingly, many, if not all, of these cooperative decisions are made with a degree of risk, that is, we often perform the cooperative acts unsure if these efforts will be reciprocated by others, either immediately or in the future. Nonetheless, cooperative acts are pervasive in human society [1], and research across a wide variety of fields has attempted to understand the motivations underlying these important social decisions. In this review, we will explore how neuroscientific research on cooperation has added to this body of knowledge, and illustrate how a better understanding of the neural mechanisms of these types of decisions can further illuminate the processes of cooperation. In addition, we discuss how these findings can potentially contribute to the development of more effective policy campaigns designed to promote cooperative decisions in the public interest.

Here we define cooperation quite broadly, essentially as any behavioral act that entails a degree of self-sacrifice to further the greater good. This could also include acts of altruism, reciprocity, and other more subtle social decisions. Clearly it is extremely important to delineate the underlying motivations that lead to cooperative behavior, both from the perspective of theory development as well as to inform practical issues of policy intervention. Neuroscience has an important role to play in this regard. Insights into the neural mechanisms of cooperation can help to better understand the psychological processes that underlie cooperative behavior, and brain research has the potential to help discriminate between theories that predict similar behavioral outcomes. For example, by disentangling the neural processes that underlie the recognition of others' intentions, neuroimaging work on action perception has proved a useful tool for critically comparing psychological theories that predict the same behavioral outcomes [2]. In a similar vein, policy makers who aim to motivate cooperation at a societal level can benefit from this approach. More comprehensive knowledge of the neural processes underlying cooperative decision-making may generate useful hypotheses as to how policy interventions could be structured, for example in relation to promoting tax compliance and the prevention of free-riding. Typically, these types of policy formulations are based on standard economic models of behavior that often do not fully represent how individuals actually decide. However, the development of more accurate, brain-based, models of decision-making has the potential to greatly help with these policy designs as they relate to our actual choice strategies.

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Introduction

One notable aspect of human social life is the degree to which we engage in cooperative interactions, either with specific identifiable others or with societal institutions more broadly. For example, we typically return favors that others have bestowed on us, such as when we help friends move house in the hope they will assist us in a similar fashion in the future. We also cooperate on a societal level — we bring our own shopping bags to the grocery store instead of taking plastic ones there, we recycle our trash to help the environment, we buy music online instead of downloading it for free, we pay our taxes when it is often easier to avoid it, and so on.

Here, we outline three lines of current research that provide useful insights into the nature of cooperative decision-making, and sketch how the advancement of these research themes can provide promising insights for the development of more effective policy campaigns.

Insight 1 – reward

Investigations of cooperative decision-making in the laboratory have typically used experimental tasks such as the Public Goods Game and the Prisoner's Dilemma, which place people in interactive settings and require them to decide about monetary allocations. These tasks are quite simple to understand and implement, but offer compelling social scenarios in which players must choose to either cooperate or not with a specific partner, or sometimes a group, with the (financial) outcomes dependent on the concomitant choices of the partners. Money in these tasks is used both as a reward in and of itself, and also as a proxy for other entitlements that people could choose to cooperate about.

Across neuroscientific studies that employ these tasks, one of the most consistent findings has been that cooperative decisions activate brain areas associated with the subjective experience of reward, namely the ventral striatum and ventromedial prefrontal cortex (VMPFC) [3–6]. One notable finding that has emerged from these studies is that this activation in reward-related neural regions is not solely the result of any monetary gain received via cooperation. Instead, it appears the act of cooperation itself can generate an increase in activation in these areas. That is, striatal activity has been shown to increase when earning a reward via a cooperative decision as compared to earning the same monetary amount in a non-social task, or even when receiving a larger reward via non-cooperation [4[•]]. Taken together with other studies on equitable decision-making and shared rewards [7,8], an important contribution from neuroscientific studies suggests that cooperation is inherently a valuable and rewarding act, over and above any objective rewards obtained via cooperative decisions [3,9].

The empirical demonstration that cooperation itself can be intrinsically rewarding has important potential relevance to policy interventions that attempt to generate and increase societal cooperation, and offers a useful example of how understanding fundamental processes can lead to practical insights. For example, the aforementioned research suggests that campaigns may have greater efficacy by triggering the intrinsic value of doing the 'right thing', and emphasizing the positive feelings that are associated with gains shared across people or groups. In addition, these studies offer some evidence that the use of incentives to promote cooperation may be more fraught than had been assumed. Typical incentive schemes often reward cooperators (e.g., by providing awards or tax benefits) and punish non-cooperators (e.g., by levying

finest or supplementary taxes), and indeed evidence from both field and experimental studies has shown that incentives can be effective in promoting cooperation [10,11]. However, the provision of incentives can backfire at times, and can result in undermining the intrinsic motivation to cooperate [12], and research examining the effect of punishment on (non)cooperative behavior has demonstrated that these threats can in fact change the brain systems recruited in cooperative decision-making [13]. These initial studies provide intriguing hints as to how we might use neuroscience to better inform our use of knowledge of the brain's reward systems to promote socially useful cooperation, and is a fruitful avenue for future research with relevant policy implications.

Insight 2 – guilt anticipation

Studies in the fields of both Psychology and Neuroscience have convincingly demonstrated via a wide variety of experimental studies that emotions have an important role to play in decision-making [14,15]. Surprisingly, however, there is little research examining the specific emotions that may be involved in cooperative decisions. One emotion that may underlie at least some decisions to cooperate is that of guilt, or more accurately, the desire to minimize guilt. That is, we may cooperate in order to avoid the guilty feelings we expect to feel if we would fail to reciprocate the generous behavior of another. In this vein, behavioral research has shown that focusing on a previous experience of guilt promotes higher degree of cooperation, and that the beliefs one has about the expectations of others can also motivate cooperative behavior [16–18].

Neuroscientific research has begun to probe this guilt hypothesis, with some initial evidence emerging from neuropsychological patients who have suffered damage to the VMPFC. These patients were shown to be specifically insensitive to the experience of guilt, and they also demonstrated less cooperative behavior [19[•]]. To extend this early finding, another group used neuroimaging in conjunction with economic modeling to construct and test a formal model of guilt aversion, and explore the neural correlates of this model [20[•]]. Here, guilt was formalized as the difference between a player's belief of what degree of cooperation was expected of them, and their actual behavior itself. A discrepancy in this difference, that is, letting one's partner down, should then lead to the experience of guilt. Results showed that players act in accordance with the expectations of others in order to minimize guilt. Neuroimaging findings demonstrated that the VMPFC plays an important role in the experience of guilt, suggesting that insensitivity to guilt may be due to an inability to form accurate expectations of other's social behavior. Importantly, increased activity in brain regions associated with negative affective states was associated with meeting the expectations of others,

indicating that the anticipation of guilt can be a powerful motivator that guides cooperative decision-making.

The knowledge that people tend to want to meet the expectations that others place on them is of great potential use for policymakers. To take advantage of the aversion to the negative experience of guilt, policy interventions could usefully be focused on heightening expectations regarding cooperative behavior. For example, social norms, which can be thought of as general expectations of how others behave, or should behave, in a given situation, can be emphasized to potentially produce increases in cooperation. Both laboratory and field studies have shown effective uses of social norms to facilitate changes in behavior. For example, exposing laboratory participants to different sets of norms concerning what type of behavior might be considered unfair can change the social preferences of participants, altering their likelihood of accepting a given allocation of money in an Ultimatum Game [21,22]. In similar vein, innovative experimental field studies have demonstrated that participant's beliefs about the decisions of others, which can be cleverly manipulated in a variety of ways, is predictive of a wide variety of everyday, real-life, behaviors, including household energy consumption [23], school bullying [24^{••}], and alcohol use [25]. Changing the perception of social norms can facilitate actual behavioral change [26–28], and policy campaigns aiming to induce cooperation could usefully endeavor to communicate a relevant norm, emphasizing the guilt that might be experienced when failing to cooperate.

Insight 3 – social ties

The previous section focused on a specific emotion, that of guilt, in understanding cooperative behavior, however a wide variety of affective states may also influence cooperation, in particular those elicited by emotional bonds [29]. For example, people typically cooperate more with others they like, or with whom they have something in common [30–32]. One mechanism that might underlie these behavioral findings of how social bonds facilitate cooperation is that of empathy. That is, emotional and social ties may foster greater empathy between individuals, which in turn may enhance cooperative behavior [33–36]. Brain imaging studies have supported this hypothesis, indicating that empathic neural responses in the insula and anterior cingulate cortex (ACC) are modulated by the behavior of others. When interacting with a non-cooperative partner, for instance, viewing that partner receiving a painful shock notably diminishes empathy-related neural activation in pain regions, including the insula and ACC [37[•]]. Additionally, empathic pain-related activations in the insula were stronger when participants witnessed an in-group member receiving shocks as compared to an out-group member [38[•]].

Another similar psychological factor that can play a role in choosing to cooperate is the ability to understand the mental states of others, often referred to as theory of mind. The brain circuitry of theory of mind processes include the dorsal medial prefrontal cortex (DMPFC), as well as regions within the parietal and temporal lobes, such as the temporoparietal junction, and posterior part of the superior temporal sulcus [39,40]. Interestingly, cooperative decisions reliably engage these neural regions, suggesting that the ability to take the perspective of another may be related to decisions to cooperate [41,42]. More compellingly, the DMPFC was shown to be heavily involved in the building of trust over time, with this activity decreasing once cooperative behavior is firmly established [43]. In a similar vein, the DMPFC was shown to encode uncertainty about a partner's belief inference, suggesting that the ability to perspective-take is indeed vital when making cooperative decisions [44].

The above results could potentially be put into practice by focusing on people's (often relatively effortless) ability to take the perspective of another, and facilitating the feelings of empathy toward others. For instance, policy interventions designed to increase social cooperation could emphasize people's shared identities, potentially by presenting the outcome of cooperation as a common, shared goal, or by asking people to imagine how they would feel when they would be in someone else's shoes. Indeed, a real-life intervention which attempted to increase registration as organ donors found exactly this, and showed that the most successful message was asking people to put themselves in someone else's position [45]. Randomized controlled trials like these, which quantitatively test the impact of theory-driven interventions, have enormous potential to tie together theory and practice, and provide important new insights that can improve policy.

Conclusion

In this brief review, we have presented an overview of how neuroscience has contributed thus far to the understanding of cooperative decision-making. Specifically, we described how insight into the neural mechanisms of reward processing, guilt anticipation, and perspective-taking can increase understanding of the nature of cooperative decision-making, and we explained how these insights may be useful for policy makers aiming to promote cooperation in everyday decision-making. However, one important caveat in the interpretation of neuroimaging results is the problem of reverse inference, namely how to identify cognitive states from patterns of observed brain activity [46]. To draw valid inferences about the engagement of a particular cognitive process, knowledge is required about which brain regions and networks are selectively associated with a particular cognitive state. However, given that a brain area can be activated by a wide range of cognitive processes, the validity of reverse inference has been increasingly

regarded as limited. One possible way to estimate selectivity of brain regions is the use of meta-analyses and large-scale databases [47]. For instance, meta-analyses have provided strong evidence that the striatum and VMPFC together constitute a general valuation system that signals the subjective value of choice during decision-making as well as outcome receipt [48,49]. Furthermore, a promising tool for interpreting brain-imaging data are on-line databases containing results of multiple neuroimaging studies, such Neurosynth [50]. The Neurosynth database can be used for large-scale automated meta-analyses of broad psychological concepts, thereby allowing researchers to conduct quantitative inferences and assess the specificity of mappings between neural and cognitive function. For instance, using Neurosynth, researchers were able to functionally distinguish three different regions within the insula and to quantitatively estimate the relative degree of functional specificity displayed by each subregion [51].

Although the use of neuroimaging is clearly very much in its infancy in relation to describing how, and why, people tend to cooperate, we believe that this approach nevertheless has great potential. By combining meta-analysis with cleverly designed behavioral tasks, neuroimaging findings can provide novel, data-driven, hypotheses that can be subsequently tested in follow-up experiments. This way, neuroscientific techniques have great promise in better clarifying societally relevant important decisions, and offer additional benefits in designing and implementing policy interventions to improve cooperation in the real world.

Conflict of interest

The authors state no conflicts of interest.

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