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A Value-Based Framework for Understanding Cooperation

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Abstract
Understanding the roots of human cooperation, a social phenomenon embedded in pressing issues including climate change and social conflict, requires an interdisciplinary perspective. We propose a unifying value-based framework for understanding cooperation that integrates neuroeconomic models of decision-making with psychological variables involved in cooperation. We propose that the ventromedial prefrontal cortex serves as a neural integration hub for value computation during cooperative decisions, receiving inputs from various neurocognitive processes such as attention, memory, and learning. Next, we describe findings from social and personality psychology highlighting factors that shape the value of cooperation, including research on contexts and norms, personal and social identity, and intergroup relations. Our approach advances theoretical debates about cooperation by highlighting how previous findings are accommodated within a general value-based framework and offers novel predictions.

Keywords
cooperation, preferences, norms, social neuroscience, neuroeconomics

Cooperation is a central feature of group living and involves any action that benefits other people while incurring a potential cost to oneself (Rand & Nowak, 2013). Human cooperation emerges very early in life and is necessary for the healthy functioning of teams, organizations, and nations as well as for solving pressing crises such as climate change. Different disciplines address the problem of cooperation. Whereas the field of neuroeconomics aims to find the neural correlates of cooperative decision-making, social and personality psychology studies how contextual factors and individual differences can influence cooperation. We outline a framework that allows for integration across disciplinary boundaries with the goal of providing a comprehensive view of human cooperation that paves the way for further interdisciplinary research (see Fig. 1a).

We first briefly summarize what is currently known about the neural encoding of value and the inputs that modulate it, highlighting processes relevant for cooperation. Although the contributions of the neural areas discussed are still areas of active research, we describe the standard model, one that will serve as a useful road map for psychologists and help promote cumulative science. In the main section of the article, we consider broader cognitive and social factors that shape value and influence it in a cooperative context. Finally, we lay out potential opportunities for research under this integrative approach and develop novel predictions.

Social Dilemmas as a Tool to Study Cooperation

Cooperation—unlike altruism—does not necessarily incur costs to the individual; nevertheless, researchers prefer to study it in the context of social dilemmas in which self-interest is directly pitted against collective interest. Social dilemmas are prevalent in everyday life, have serious consequences, and provide researchers a chance to disentangle and quantify underlying competing

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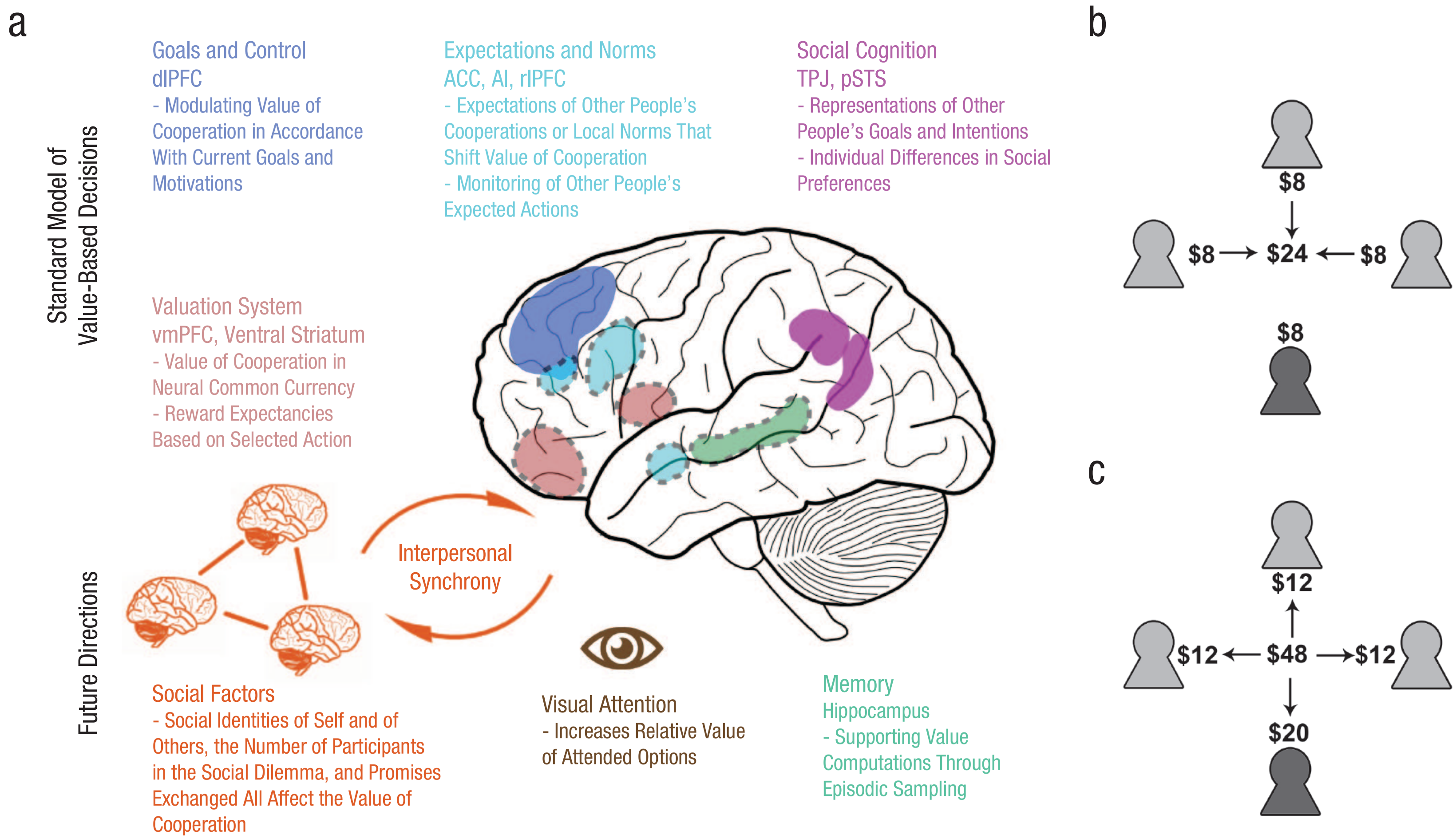

Fig. 1. Summary of the value-based framework for cooperation (left) and example trial from a public-goods game (right). The schematic of the value-based framework for cooperation (a) shows known modulatory inputs (top row) that affect the computation of cooperative value (middle row). These inputs include goals and control, expectations and norms, and social cognition. The bottom row shows new avenues for research originating in social and cognitive psychology and neuroscience, including social factors, visual attention, and memory. These factors are implemented in various regions shown in the brain image and modulate the value system, which is implemented in the ventromedial prefrontal cortex (vmPFC) and ventral striatum. In a social dilemma such as the public-goods game, players are faced with tension between cooperating and benefiting the collective or acting selfishly. Players are given an initial allocation of money and can either keep it or contribute it to the common good (b). Money contributed to the common good is multiplied by some factor (here, 2) and then equally redistributed to all players (c). The noncooperative player (dark gray) receives a higher total payoff than the cooperative players (light gray). However, collective gains would have been maximized if all players had cooperated. dlPFC = dorsolateral prefrontal cortex; ACC = anterior cingulate cortex; AI = anterior insula; rlPFC = right lateral prefrontal cortex; TPJ = temporoparietal junction; pSTS = posterior superior temporal sulcus.

motivations (Bowles & Gintis, 2013). The primary tools of cooperation research are economic games that model social dilemmas by creating conditions for costly prosocial and cooperative behavior under controlled conditions (see Fehr & Camerer, 2007). For example, the public-goods game or the prisoner's dilemma (see Figs. 1b and 1c) model social dilemmas in which if everyone acts selfishly, everyone is worse off. Cooperation is a type of prosocial behavior, along with altruism and fairness (e.g., studied in the dictator game or ultimatum game[1]). Because the neural correlates of prosociality have been more widely investigated (Ruff & Fehr, 2014), we draw from findings across the literature under the assumption that similar neural circuitry is involved.

Social dilemmas require a consideration of self- and other-regarding motivations, which are captured by the concept of *social preferences*, which refers to how people value outcomes to themselves and others (Fehr & Camerer, 2007). Social-preference models contain parameters that capture the trade-off between self- and other-regarding concerns during social dilemmas (Fehr & Schmidt, 1999). These parameters are flexible enough to account for different phenomena—including endogenous motives, such as the "warm glow" one gets from acting cooperatively (Andreoni, 1990), as well as exogenous motives, such as the threat of peer punishment for defecting—that are known to increase and maintain cooperation over time (Fehr & Gächter, 2002; Fehr & Schurtenberger, 2018). By considering cooperation as a computational process weighing costs and benefits for the self and others, one may factor in punishment probability as a cost to oneself when choosing to defect. A large probability of punishment may therefore trump the temptation of defection and tip the chooser toward cooperation. Here, we frame our discussion in terms of how the value of cooperation is constructed and the various sources of its modulation, including exogenous motivations to cooperate, such as threats of punishment or threats to one's reputation.

Value-Based Framework for Cooperation

Valuation system

To make any decision, from reviewing scientific articles to cutting in line, the brain must assign and compare values for all the available options in a domain-general neural code or *common currency*. These subjective values can then be compared, traded off, and used to guide decisions and goal-directed behavior. Studies have established that value computation and representation occurs within the ventromedial prefrontal cortex (vmPFC), the orbitofrontal cortex,[2] and the ventral striatum (Levy & Glimcher, 2012). Our framework assumes that cooperation and defection use the same neural circuitry to assign subjective values and make decisions.

Evidence suggests that cooperation engages the value system. Studies have found vmPFC activity when people choose to donate, act fairly, and cooperate, and both vmPFC and ventral striatum respond more strongly to equality than inequality (Cutler & Campbell-Meiklejohn, 2019; Fehr & Camerer, 2007; Ruff & Fehr, 2014). Alternatively, lesions to the vmPFC reduce prosocial behavior and the guilt associated with it (Krajbich, Adolphs, Tranel, Denburg, & Camerer, 2009). Thus, the overall subjective value of cooperation, the combination of motives and payoffs characterizing these dilemmas, is represented in the value system.

Subjective value is constructed using inputs from multiple brain regions, including areas associated with basic cognitive processes and social functions. For example, the presence or absence of extrinsic rewards for cooperation elicits altruistic or strategic modes of cooperation that rely on distinct neural computations (Cutler & Campbell-Meiklejohn, 2019). Such inputs can flexibly alter behavior to accommodate changing contexts and preferences and eventually tip the balance toward selfish or cooperative choices. In the next section, we discuss these inputs.

Value modulation

Executive control. Executive control, implemented by the dorsolateral prefrontal cortex (dlPFC), modulates subjective value representations, allowing higher-order goals or motivations to shape and override existing valuations. In the case of cooperative decision-making, the dlPFC flexibly implements context-specific social goals and adjusts values of actions and outcomes to promote those goals (Carlson & Crockett, 2018; Tusche & Hutcherson, 2018). Supporting this view, recent findings show that participants who tended to act cooperatively showed greater vmPFC activity when cooperating and heightened dlPFC activity and dlPFC-vmPFC connectivity when acting selfishly (Wills, Hackel, & Van Bavel, 2018). Participants who tended to act selfishly showed the opposite pattern. Moreover, the same research found that people who were highly sensitive to group norms exhibited greater dlPFC-vmPFC connectivity when defying group norms. Thus, executive control, implemented by the dlPFC, may facilitate or inhibit cooperation depending on the individual's current context and goals.

Social learning and social norms. The decision to cooperate depends on learning about the social context to build expectations of what other people will do. Most people exhibit conditional cooperation: They cooperate if others cooperate and defect if others defect (Fehr & Schurtenberger, 2018). Thus, experimentally manipulating expectations alters the likelihood of accepting unfair offers (Chang & Sanfey, 2011; Xiang, Lohrenz, & Montague, 2013), a process associated with the anterior cingulate cortex and anterior insula. Similarly, learning about local fairness norms plays a key role in determining cooperation (Xiang et al., 2013). Thus, learning and updating expectations is central to cooperation.

Representing social norms and acting on them is another crucial process underlying cooperative behavior, and the insula appears to play an important role in achieving it. For example, patients with insula lesions display reduced rates of internal norm updating, a behavior crucial for sustaining cooperation (Gu et al., 2015). The insula is also linked to fairness representation: Unfair offers elicit insula activation, and this response is correlated with the likelihood of rejecting such offers (Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). Even without direct benefit to the chooser, insula activity negatively correlates with levels of inequity (Hsu, Anen, & Quartz, 2008), and the pattern of activity tracks individual differences in inequity aversion. Compliance with social norms, whether voluntarily or under the threat of punishment, causally involves the right lateral prefrontal cortex (Ruff, Ugazio, & Fehr, 2013). Taken together, neural representation of norms and expectations, acting in accordance with them, and monitoring deviations from them allow for dynamic cooperation decisions over time.

Individual differences. Individual variation in social preferences also modulate the value of cooperation (Van Lange, De Bruin, Otten, & Joireman, 1997). Activity in the social-cognition network, including the temporoparietal junction (TPJ) and the adjacent posterior superior temporal sulcus (pSTS), is implicated in the representations of other people's minds, goals, intentions, and social distance (Parkinson, Kleinbaum, & Wheatley, 2017). In the context of cooperation, functional and anatomical properties of these areas may be linked to individual differences in social preferences (Morishima, Schunk, Bruhin, Ruff, & Fehr, 2012). For example, when choosing charitable donations, activity in the pSTS correlates with overall willingness to give (Hare, Camerer, Knoepfle, O'Doherty, & Rangel, 2010). Moreover, functional connectivity between the TPJ and vmPFC may be how people incorporate social preferences into value computations and increase prosocial behavior (Strombach et al., 2015). Thus, these areas appear to contribute social information during cooperation decisions by sending modulatory signals to the value system.

Current and Future Directions in Cooperation Research

The value-based framework can add conceptual clarity and help guide and interpret research on cooperation. However, many nuances of human interaction are not well represented in the standard model. We argue that this can be addressed by marrying it with research lines from cognitive and social psychology as well as recent technological advances.

In this section, we highlight several areas in which the value-based approach could benefit from other disciplines and vice versa. First, we discuss how additional cognitive capacities that influence decision-making can inform the value-based framework. Second, we discuss how social-psychological approaches to cooperation can be organized and integrated into the value-based framework. Third, we discuss how the fundamentally social nature of cooperation warrants research methods and approaches involving more realistic interactions and how the value-based framework is situated to interpret results from such investigations.

Memory

The value-based framework assumes that cooperative values are constructed on the basis of multiple modulatory inputs to the core valuation system. A basic assumption has been that the value of cooperative actions is maintained primarily through associations acquired through basic reinforcement learning. Recent work has found a link between episodic memories in the hippocampus and value-based decision-making implemented by sampling related episodic memories (Shadlen & Shohamy, 2016). Hippocampal connectivity with the striatum and vmPFC biases value-based decisions for monetary rewards (Shadlen & Shohamy, 2016; Wimmer & Shohamy, 2012). We hypothesize that the hippocampus might be similarly involved in cooperative decisions, possibly by recalling the results of previous cooperation or memories of specific interaction partners to compute the expected value of cooperation. Indeed, recent evidence suggests that imagining prosocial acts through episodic simulation can increase prosociality (Gaesser & Schacter, 2014).

If the value of an action in a given situation is partly constructed by recalling past episodes (Bornstein, Khaw, Shohamy, & Daw, 2017), then the value of cooperation may be biased by priming specific past interactions. Thinking about a time someone acted cooperatively (or was rewarded for cooperating) might increase the value of cooperation in a current, unrelated social dilemma. However, because memory declines over time along with the influence of episodic memories on value computations (Levin, Fiedler, & Weber, 2019), temporally distant cooperative events may not be integrated in current decisions affecting how cooperation is valued. Thus, not only are more distant or forgotten memories of cooperative events less likely to modulate value computations (unless primed), but also as cognitive decline ensues, misremembered memories may alter the value computation. Together, this implies that understanding the role of the hippocampus for cooperation promises to lead to a better understanding of the core process constructing value.

Attention

Momentary fluctuations in attention also modulate value. For example, fixating toward an option increases the likelihood of choosing it (Smith & Krajbich, 2018), and value signals in the striatum and vmPFC are modulated by relative fixation time to options (Lim, O'Doherty, & Rangel, 2011). Moreover, manipulating how long people fixate on different options can alter decision-making (Pärnamets et al., 2015), although more research is needed to determine whether guiding attention can have a causal effect on social decisions (Ghaffari & Fiedler, 2018). Nevertheless, instructing participants on what features in a social decision to attend to has been found to influence weights given to payoffs to themselves as opposed to others when they make decisions in a modified dictator game (Tusche & Hutcherson, 2018). We propose that visual fixations will similarly modulate value representations when people decide to cooperate. For example, attending to known cooperators might increase the value placed on cooperation either by bringing to mind past experiences of cooperation or by activating other-related preferences in the TPJ. Critically, individual differences in the value of cooperation can become apparent from the impact attention may have on choice. For example, in an individual who places a low value on cooperation, attention to cooperating individuals might amplify that valuation, further decreasing the likelihood of a cooperative decision. Nevertheless, if attention does affect cooperation in a predictable manner, then it might also be possible to alter decisions by manipulating attention, whether exogenously or endogenously.

Identity

Humans use group membership to navigate social landscapes. Depending on the social context, different identities are made salient, differentiating the in-group from out-groups (see Turner, Oakes, Haslam, & McGarty, 1994). This is important because people cooperate more with in-group than out-group targets (Brewer & Kramer, 1986; Yamagishi & Kiyonari, 2000). Moreover, observing an in-group member win money is subjectively more rewarding compared with observing an out-group member win money, and this subjective reward correlates with more activity in the vmPFC (Hackel, Zaki, & Van Bavel, 2017). These findings raise the possibility that identity might increase cooperation through a direct influence on the value of cooperation. Group identity might also influence cooperation through other social representations, such as norms, expectations, and interdependence (Balliet, Wu, & De Dreu, 2014), which correlate with the weight assigned to social partners during prosocial choice (Hutcherson, Bushong, & Rangel, 2015). Given the fundamental role identity plays in regulating social behavior, understanding how this influence plays out in valuation-based circuitry will be important to integrate social psychological and neuroeconomic approaches in order to better understand cooperation.

Understanding the role of identity through the lens of value-based decision-making can also help resolve outstanding questions on how group membership affects cooperation. For example, there are mixed findings on the effects that group size plays. Experiments and theoretical simulations present evidence for both increasing and decreasing cooperation with group size (Pereda, Capraro, & Sánchez, 2019). One reason for these mixed findings might be that size alone might not be the relevant variable determining cooperative value. Not all groups are created equal; a group of 20 of your best friends will not invoke the same levels of cooperation as a group of 10 farmers from a distant land. Instead, identification with the group will activate different norms (Bicchieri, 2002; Brewer & Kramer, 1986). If our hypothesis is correct, then group size should not generally correlate with subjective value of cooperation in the vmPFC but instead be reflected in activity associated with modulatory inputs from norm and expectation encoding.

Social interaction

Cooperation occurs in many settings, and experiments on social dilemmas often trade off realism in the interactions for experimental control. Thus, much of what is known about the neural processes underpinning value-based decisions comes from studies on isolated individuals. Yet more naturalistic interactions can provide novel insights into cooperation. For example, past research has found that allowing players to communicate can have large, positive effects of cooperation (Janssen, Holahan, Lee, & Ostrom, 2010). Similarly, allowing players in public-goods games to make a nonbinding promise, known as *cheap talk*, leads to higher rates of cooperation (Balliet, 2010). We argue that the value-based framework can help researchers understand how these cooperative decisions were formed. For instance, cheap talk may activate both expectations of group cooperation and norms surrounding promise keeping (Bicchieri, 2002). Future research should do more to create realistic situations for studying cooperation.

A critical avenue for refining explanatory scope under realistic conditions comes from technological advances, such as simultaneous brain-imaging technology. For example, interbrain synchrony between two people, recorded using electroencephalography, predicts decisions to cooperate in a face-to-face social dilemma (Jahng, Kralik, Hwang, & Jeong, 2017). These synchrony effects were located to activity in the temporoparietal regions, possibly indicating the TPJ's involvement in representing the social partner. Interbrain synchrony is also associated with dyads' decisions to cooperate in cooperative as opposed to noncooperative contexts (Hu et al., 2018). Nevertheless, the causal link between cooperation and interbrain synchrony remains an area for future research. Interbrain synchrony between people might reflect shared attention, coordinated joint actions, or shared mental representations. A value-based framework will allow findings resulting from measuring neural activity from multiple individuals to be parsimoniously interpreted and integrated into a wider science of cooperation.

Conclusion

Adopting a value-based framework holds promise for understanding how different people in different contexts make cooperative decisions. This approach not only has explanatory power to organize current findings but also offers to bridge several literatures under a common framework, providing what we hope is a more complete and enduring explanation of behavior. If this approach can harness the collective intelligence of scientists and scholars from philosophy to neuroscience, it will allow them to cooperate on solving a long-standing scientific debate as well as some of the most pressing problems facing humanity.

Recommended Reading

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Transparency

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Notes

1. The dictator game endows money to one person who decides whether to send money to a partner. The ultimatum game endows money to a proposer, who decides how much to split with another player. If the other player accepts the deal, the money is split per the proposal. If the other player rejects the deal, neither player receives money.
2. For simplicity, we will use *vmPFC* to mean either vmPFC or medial orbitofrontal cortex throughout the article.

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