Brain and Cognition 81 (2013) 95–117

Contents lists available at SciVerse ScienceDirect

Brain and Cognition

journal homepage: www.elsevier.com/locate/b&c

Theoretical Integration

When do people cooperate? The neuroeconomics of prosocial decision making

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ARTICLE INFO

Article history:
Accepted 10 September 2012
Available online 20 November 2012

Keywords:
Neuroeconomics
Social dilemmas
Social preferences
Cooperation
Altruistic punishment

ABSTRACT

Understanding the roots of prosocial behavior is an interdisciplinary research endeavor that has generated an abundance of empirical data across many disciplines. This review integrates research findings from different fields into a novel theoretical framework that can account for when prosocial behavior is likely to occur. Specifically, we propose that the motivation to cooperate (or not), generated by the reward system in the brain (extending from the striatum to the ventromedial prefrontal cortex), is modulated by two neural networks: a cognitive control system (centered on the lateral prefrontal cortex) that processes extrinsic cooperative incentives, and/or a social cognition system (including the temporo-parietal junction, the medial prefrontal cortex and the amygdala) that processes trust and/or threat signals. The independent modulatory influence of incentives and trust on the decision to cooperate is substantiated by a growing body of neuroimaging data and reconciles the apparent paradox between economic versus social rationality in the literature, suggesting that we are in fact wired for both. Furthermore, the theoretical framework can account for substantial behavioral heterogeneity in prosocial behavior. Based on the existing data, we postulate that self-regarding individuals (who are more likely to adopt an economically rational strategy) are more responsive to extrinsic cooperative incentives and therefore rely relatively more on cognitive control to make (un)cooperative decisions, whereas other-regarding individuals (who are more likely to adopt a socially rational strategy) are more sensitive to trust signals to avoid betrayal and recruit relatively more brain activity in the social cognition system. Several additional hypotheses with respect to the neural roots of social preferences are derived from the model and suggested for future research.

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1. Introduction

The high level of voluntary cooperation in social interaction can be considered as one of the unique and defining human features. Teamwork and collective action have undeniably contributed greatly to the success of economy-based societies. But as cooperation often involves a reciprocal exchange of benefits in an interdependent fashion, it also provides an opportunity for exploitation. Some people may be tempted to free-ride on the cooperation of others, and hence profit from cooperative benefits without contributing. Such opportunistic behavior may easily undermine the effectiveness of cooperative action, and poses a challenge to evolutionary and economic explanations of cooperative behavior, especially in exchange situations where one has the choice between a self-interested strategy versus a strategy that benefits the whole group, but at a personal cost. Classic economic theory predicts that a *Homo economicus*, who compares the costs and benefits of different courses of action, will not cooperate given this dilemma. However, if no-one cooperates, everyone is worse off (Dawes & Messick, 2000). Yet an abundance of field and experimental research has revealed that in all cultures people are willing to pay the cost of cooperation, even in anonymous situations where the probability of future repayment is zero (Henrich et al., 2005).

This cooperation dilemma has sparked researchers in many scientific domains to pool their efforts in order to understand why costly prosocial behavior persists despite the high levels of uncertainty intrinsic to many social exchanges. The search for the roots of human cooperation has produced two mostly independent streams of research that have revealed two fundamentally different logics behind prosocial behavior, one claiming that cooperation is economically rational, the other that it is socially rational. Following *economic rationality*, cooperation is the product of natural selection acting on the individual (Hagen & Hammerstein, 2006). People are naturally motivated to pursue self-interest, but cooperate readily when self-interest coincides with collective interest. Hence this research stresses the importance of extrinsic incentives that align self- and collective interest prompting people to act prosocially to reap personal benefits from cooperative interactions (e.g., Bornstein, 2003; Kollock, 1998).

Adherents of *social rationality* consider cooperation to be compatible with theories of group selection (e.g., Sober & Wilson, 1998; Wilson & Sober, 1994). People are intrinsically motivated

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0278-2626/$ - see front matter © 2012 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.bandc.2012.09.009

to cooperate and feel good doing so, because the cooperative default has been selected in evolution due to the benefits that accrue in the group. Showing one's willingness to cooperate is thereby an effective way to strengthen belonging, build social networks, and avoid ostracism (Caporael, Dawes, Orbell, & Vandekragt, 1989). However, a group of cooperating individuals is very vulnerable to invasion by free-riders. Therefore, research on social rationality stresses the importance of trust in social interaction (e.g., Markoczy, 2004; Haselhuhn & Mellers, 2005; Yamagishi, 1998; Yamagishi & Sato, 1986), and the threat of ostracism which may result from breaches of trust (Williams, 2007).

The purpose of this review is to develop a theoretical framework that integrates these two contrasting views regarding the rationality behind cooperation. Specifically we advance two new and general propositions. First, we propose that economic and social rationality are not contradictory for the brain, but that we are in fact wired for both. Economically and socially rational choices are rooted in different neural networks that operate in concert and independently modulate decision making. Cooperative decisions can be explained as motivated choices that yield either economically valuable or social rewards. However, these choices are contingent on the presence of extrinsic incentives that align self- and collective interest (following economic rationality), and/or trust signals that minimize the chance of exploitation (consistent with social rationality). Therefore, brain systems that process extrinsic incentives and trust are expected to modulate the willingness to cooperate. The second proposition is that individual differences in self- versus other-regarding preferences coincide with economic and social rationality and influence the relative extent to which these brain networks will be recruited in cooperative decision-making.

To create an overarching model that spans both the external events and the neural networks influencing prosocial behavior (e.g., Beauchamp & Anderson, 2010), we rely on current research in the new and growing field of neuroeconomics, a joined effort of psychologists, neuroscientists, and behavioral economists with the primary purpose of opening the "black box" of human decision making. The neuroeconomic approach combines the rigorous experimental paradigms from game theory with neuroimaging techniques in order to identify the brain regions that are recruited during decision-making (Camerer, 2008; Camerer, Loewenstein, & Prelec, 2005; Kahneman, 2003). Neuroimaging experiments that investigate choice behavior in combination with contextual influences and individual motives are able to reveal the interplay between affective and cognitive processes that influence conscious deliberation. With this approach we hope to fine-tune the "rational choice" behind cooperation and present a framework for solving social dilemmas that incorporates both economically and socially rational motives, resolving the paradox that emerged in the cooperation literature.[1]

This review is organized as follows. We begin by outlining the two contrasting views in the literature – one based on economic, the other on social rationality – that associate cooperative behavior with (respectively) extrinsic incentives or trust. Next, we propose a neural model that incorporates the modulatory role of extrinsic incentives and trust in generating a prosocial decision in the face of uncertainty (e.g., in a social dilemma that offers a cooperative versus a self-serving choice). We also propose a second model that identifies the brain systems that are recruited when prosocial norms are violated, as this tends to lead to altruistic punishment. The latter is included because of its presumed importance in sustaining long-term cooperation (e.g., Boyd, Gintis, Bowles, & Richerson, 2003; Fehr & Gachter, 2002), and because it has generated much experimental and neuroeconomic research. We then review the individual differences in cooperative behavior and altruistic punishment. We include studies that have addressed behavior and/or neural correlates of self- versus other-regarding individuals, and investigate if their prosocial choices are associated with different patterns of brain activation. This would indicate that there are different individual drivers for prosocial behavior that correspond to distinct types of rationalities. Finally, we outline avenues for future research.

2. Economically versus socially rational reasons to cooperate

2.1. Extrinsic incentives

Most of the evidence pointing to the role of extrinsic incentives in cooperation comes from experimental economic games that simulate social dilemmas. Social dilemmas are mixed motive situations in which self-interest and fear of betrayal tend to pull people towards non-cooperation. Extrinsic cooperative incentives are ecologically relevant, context-related incentives that align self-interest with collective interest and thereby remove the temptation to free-ride and motivate people to cooperate. Thus extrinsic incentives objectively transform the pay-off matrix of a social dilemma so that cooperation becomes an economically rational choice yielding tangible rewards. Such economic motives convince even those who are not naturally inclined to cooperate.

Extrinsic incentives come in many different forms. First, realizing the benefits of long-term cooperative relationships is one of the more common reasons that compels someone to pay for an initially costly cooperative act. This is true for the "tit for tat" strategy, where a person in a dyadic interaction starts out cooperating and thereafter reciprocates all responses of the partner. When both partners end up cooperating mutually, profits accrue over time, making "tit for tat" an evolutionary stable strategy and cooperating a rational choice (Axelrod & Hamilton, 1981).

Second, when cooperation leads to synergy, as in team tasks where team members possess complementary skills, there is no conflict between self- and collective interest and cooperation becomes beneficial to all. Not surprisingly, in social dilemma games, synergy in pay-offs tends to significantly increase cooperation (Boone, Declerck, & Kiyonari, 2010; Boone, Declerck, & Suetens, 2008; Camerer & Fehr, 2006).

Third, people cooperate to acquire a reputation for being generous. Conspicuous prosocial behavior may well be a self-presentation strategy to increase one's status in a group and benefit from indirect reciprocity (Nowak & Sigmund, 2005). Corroborating this "competitive altruism" hypothesis, Hardy and Van Vugt (2006) showed that, the more generous experimental participants are in social dilemma games, the more often they are chosen as interaction partners, and the higher their status. In real life situations, generous donations to charity correspond to higher sympathy and trustworthiness scores (Bereczkei, Birkas, & Kerekes, 2007). Not surprisingly, social cues that reduce anonymity and introduce possible audience effects are very effective in increasing prosocial behavior (Kurzban, DeScioli, & O' Brien, 2007; Piazza & Bering, 2008).

Finally, sanctions that substantially increase the cost of non-cooperation make up a powerful class of negative incentives. The threat of verbal criticism, poor reputation, or monetary fines are very effective in encouraging people to abide by prosocial societal norms. Corroborating this is a large-scale experimental study across 15 different societies indicating that, for each culture, the incidence of punishment in experimental social dilemma games

[1] This study addresses the proximate reasons for cooperation and, in doing so, we try to specify how different brain systems are organized and respond to contextual input in order to generate a cooperative decision. Other recent reviews addressing the neural correlates of social interaction (e.g., Rilling & Sanfey, 2011) tend to focus on more ultimate reasons that were shaped by natural selection and allowed cooperative behavior to emerge and be sustained. In addition, the current review takes a more integrative approach by illustrating how the different brain systems involved in cooperative decision-making respond to environmental inputs and moderate each other.

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