

Review

Neuroscientific approaches to study prosociality

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Abstract

Prosociality is a core feature of human functioning and has been a topic of interest across disciplinary boundaries for decades. In this review, we highlight different neuroscientific approaches that have enriched traditional psychological methods for studying prosocial behavior among individuals and groups. First, we outline findings from task-based neuroimaging studies that provide correlational evidence for the involvement of different neural mechanisms in prosocial behavior. Next, we present different brain stimulation studies that show several brain areas to be causally related to prosocial behavior. Furthermore, we outline the task-independent neural trait approach that quantifies temporally stable brain-based characteristics in an effort to uncover sources of interindividual differences in prosocial preferences. We discuss how the findings from these approaches have contributed to our understanding of prosocial behavior and suggest directions for future research.

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Introduction

Prosocial behavior — defined as a broad range of actions intended to benefit another person or group [1] — is pivotal for maintaining interpersonal relationships at multiple scales [2, 3], thereby contributing to the emergence and thriving of small to large-scale societies [4, 5]. Understanding how prosocial behaviors originate, develop, and vary across individuals, groups, and

contexts, has been a challenging research endeavor across various disciplines.

In recent years, the interest in studying prosocial behavior from a more comprehensive perspective including the integration of insights from neuroscience into psychological and related research has grown. Incorporating neural levels of analysis into the study of human prosociality has, for example, enabled us to unveil hidden prosocial motives, identify processes that differentiate between competing theories of social behavior, and build more extensive models allowing improved predictions about human behavior. In particular, three neuroscientific approaches have been influential in expanding our understanding of prosocial decision-making. First, task-based brain imaging studies have allowed us to identify neural activity in specific brain regions or during a specific time that are functionally involved in the execution of a given task, thereby informing us about potential processes underlying prosocial decision-making. Second, brain stimulation research has enabled us to establish causal relationships between prosocial behavior and the functioning of specific brain areas. Third, task-independent brain imaging has provided us with neural trait markers to investigate potential sources of interindividual variability in prosocial behavior.

In this review, we will provide an overview of these approaches and introduce the most commonly applied neuroscientific methodologies. Furthermore, we will highlight relevant findings that have emerged from these approaches and discuss how they have shed light on the mechanisms underlying human prosociality. Finally, we propose directions for future research.

Task-based brain imaging: examining neural processes

One way to study the complex processes underlying prosocial decision-making is through task-based ‘online’ brain imaging, which involves recording participants’ brain activity while they engage in social decision-making tasks. These tasks commonly model the complexity of real-life situations in the form of experimental games, which allow for measuring actual prosocial behavior in controlled experimental settings (for an overview, see van Dijk and De Dreu [6] and Van Lange et al. [7]). Here, we focus on functional magnetic resonance imaging as this is the most routinely and commonly used technique in this field. It provides

images of the neural activity in the brain, which is estimated using the blood oxygen level (BOLD response), showing which regions of the brain are more active during the execution of a task.

In an effort to unravel the neural processes underlying prosocial decision-making, Bellucci et al. [8] tried to identify brain regions consistently activated across different types of prosocial behavior. Using 600 neuroimaging studies, they found that neural activation patterns of prosocial behavior partially overlap with mentalizing and empathy networks, such as the dorsal posterior and middle cingulate cortex, and — in self-serving inequality — the temporoparietal junction (TPJ). Moreover, they showed that prosocial behavior consistently recruits brain regions such as the ventromedial prefrontal cortex (vmPFC) and the dorsolateral prefrontal cortex (dlPFC). These findings suggest that prosocial behavior comprises not only mentalizing and empathetic abilities that enable individuals to understand others' needs and increase the motivation to help, but also involves processes such as valuation (vmPFC), planning, and cognitive control (dlPFC).

In another meta-analysis, Cutler and Campbell-Meiklejohn [9] examined whether neural activation patterns differ depending on the type of a prosocial act. They found that although both altruistic and strategic giving commonly activate brain regions in the reward and value-computation networks, the two types of giving are supported by distinct neural regions. For example, strategically motivated prosocial acts (i.e., with the prospect of improving one's situation via reputation or reciprocity) are associated with greater activity in striatal regions and the dlPFC, whereas nonstrategic (i.e., intrinsically rewarding, purely altruistic) decisions show greater activity in the posterior vmPFC. In other words, the presence or absence of extrinsic rewards for prosocial behavior seems to involve different neural computations, leading to different prosocial choices [9, 10].

Thus, neuroimaging evidence shows that prosocial behaviors consistently recruit a specific set of brain regions dedicated to social cognition, cognitive control, as well as reward and value processing. However, there is also converging evidence showing that the involvement of specific brain areas in prosocial choices depends on the strategic nature of a prosocial act [9], and — as further research shows — on differences in personality characteristics [11–13]. For example, Hackel et al. [11] recently found that individuals with prosocial traits show greater vmPFC activity when acting prosocially, as well as heightened dlPFC activity and dlPFC-vmPFC connectivity when engaging in a selfish act, whereas selfish individuals showed the opposite pattern. Hence, cognitive control implemented by the dlPFC may encourage or inhibit prosocial behavior depending on an individual's prosocial traits and the context in which a

decision occurs [10, 11]. This taps into a long-standing debate about whether prosocial behavior reflects an intuitive first reaction, or a second, more deliberate reaction [14–16]. Looking at this dichotomy from a neuroscientific perspective, research points to a more integrative framework: rather than regarding prosociality as a universally prepotent or deliberative reaction, it appears that prosocial decisions strongly hinge on the interaction between individual characteristics and situational constraints [2, 10, 17].

Although studies using brain imaging have yielded many fruitful insights into the mechanisms underlying human prosociality, these methods primarily provide correlational information about the relationship between brain areas and prosocial decisions. In the next section, we therefore turn to noninvasive brain stimulation methods, such as transcranial magnetic stimulation (TMS) and transcranial electrical stimulation, which enable us to directly modulate brain activity and thereby establish causal brain-behavior relations.

Noninvasive brain stimulation: inferring causality

Advances in noninvasive brain stimulation technologies over the last decades have equipped us with tools to safely modulate the brain by inducing changes in cortical excitability. TMS induces a magnetic field by passing an electrical current through a conductive coil, using individual, paired, or longer trains of regularly spaced pulses. Transcranial electrical stimulation, on the other hand, refers to a broad range of different techniques that involve passing relatively weak currents through the skull, thereby modulating the likelihood of action potentials to occur. One of the most common transcranial electrical stimulation methods is transcranial direct current stimulation (tDCS), where a current of a constant magnitude passes between two or more electrodes positioned on the scalp. This current causes a subthreshold modulation of the resting membrane potential of cortical neurons, thereby typically increasing (anodal tDCS) or decreasing (cathodal tDCS) their likelihood of firing [17]. Another approach is to influence intrinsic oscillatory neural activity by varying the amplitude and polarity of the current, which can be achieved using transcranial alternating current stimulation (for reviews on noninvasive brain stimulation methods, see for example [18–20]).

As noninvasive brain stimulation methods are generally limited to the modulation of brain areas lying not more than a few centimeters away from the cortical surface [18, 21], studies examining the causal involvement of neural processes in prosociality typically target cortical brain areas, such as the vmPFC (associated with, e.g., value computation), dlPFC (associated with, e.g., behavioral control), or TPJ (associated with, e.g., perspective-taking). For example, Soutschek et al. [22]

found that participants who received inhibitory TMS over the TPJ behaved more selfishly than participants with a vertex stimulation as a control site. Similarly, Li et al. [23] applied anodal tDCS (i.e., increasing the cortical excitability) over participants' TPJ, while they allocated financially rewarding tokens between themselves and a charity. They found that enhancing cortical excitability in the TPJ increased participants' charitable giving, thereby providing further evidence for the causal involvement of the TPJ in prosocial behavior. In addition, research has also shown that enhancing cortical excitability of the vmPFC increases both prosocial giving [24] and punishing unfair behaviors at a personal cost [25].

Other studies have focused on the causal link between the dlPFC and prosocial decision-making. For example, research has demonstrated that applying inhibitory TMS [26] or cathodal tDCS [27] over the dlPFC leads to increased selfishness, whereas stimulating the dlPFC using anodal tDCS or excitatory TMS increases prosocial decisions [28–30]. However, other research also shows that inhibitory TMS increases prosocial giving [31], which points to a more nuanced role of the dlPFC in prosocial decision-making that may — in line with insights from neuroimaging studies outlined previously — be sensitive to situational and individual characteristics. Providing causal support for this assumption, Gross et al. [32] found that whether brain stimulation over the right dlPFC increases or decreases selfishness depends on both external rules (i.e., a rule that demands to make self- or other-serving monetary allocations) and individual personal goals (i.e., unrestricted behavior used as a proxy for internal motives). More precisely, cathodal tDCS increased participants' willingness to follow rules, even if these rules demanded to hurt oneself or others financially, whereas anodal tDCS led participants to violate rules more often that were at odds with their free choices.

Taken together, these findings present causal evidence showing that activity in brain areas including the theory of mind network, valuation system, and lateral prefrontal cortex underlies prosocial decision-making. Furthermore, these results support neuroimaging findings showing that the dlPFC does not generally inhibit prosocial or selfish choices but plays a crucial part in reacting to internal values and contextual constraints. This indicates that exploring sources of interindividual differences in prosocial motives and responses to external variables may significantly contribute to our understanding of human prosociality. The neural trait approach, outlined as follows, is an important attempt to explain this interindividual variation.

Task-independent brain imaging: explaining interindividual variability

People exhibit substantial interindividual variability in their prosocial tendencies [33, 34]. One promising way

to uncover sources of behavioral heterogeneity in prosociality is through the neural trait approach. This approach seeks to explain sources of behavioral heterogeneity with task-independent 'offline' brain-based characteristics that are objective and stable over time (i.e., neural traits [17]). One neural trait measure is resting-state electroencephalogram, which measures neural baseline electrical activity when participants are at rest. This activity can be characterized, for example, by power values for different frequency bands or electrical microstates [35]. Another neural trait measure can be derived from structural magnetic resonance imaging by looking at neuroanatomical differences in gray matter (i.e., cortical volume and thickness) or white matter (i.e., structural connections).

Using a neural trait approach, Morishima et al. [36] first demonstrated a positive link between gray matter volume in the right TPJ and individuals' prosociality in situations of self-serving inequality. More recently, baseline activation in the right TPJ has been linked to increased conditional cooperation (i.e., individuals who cooperate if others also cooperate), unconditional cooperation [37], and compliance with fairness norms [38]. Furthermore, based on a behavioral study showing that humans display a 'cooperative phenotype' in the sense of a temporally stable and general inclination toward prosocial behavior [39], Gianotti et al. [40] examined whether neural signatures underlie individual differences in this phenotype. Indeed, they found that task-independent baseline activation in the TPJ was associated with interindividual variation in domain-general prosociality (i.e., prosociality across different situations). Together, these studies suggest that — even across different situations — people with higher baseline activation of the TPJ consistently behave more prosocially than others, possibly due to increased abilities in mentalizing and overcoming self-centeredness [22, 41].

Other neural trait studies found that baseline activation and/or volume of the orbitofrontal cortex [42], dlPFC [38, 43, 44], and anterior insula [45] were associated with individual differences in prosocial decision-making. For example, Baumgartner et al. [37] showed that conditional cooperators displayed higher baseline dlPFC activation than unconditional cooperators or non-cooperators. Similarly, Gianotti et al. [38] found higher baseline activation in the dlPFC in individuals who complied with fairness norms when facing potential sanctions (i.e., sanction-based compliers) compared with individuals never complied. These findings thus suggest that higher dlPFC baseline activation may enable conditional and sanction-based cooperators to strategically adapt their behavior to changing situations, providing further evidence that neither prosocial nor selfish behavior is universally 'default' but depends on an individuals' personality and context.

Conclusion and future directions

The many studies combining neuroscience with psychological and related research have provided valuable insights into the neural underpinnings of prosociality, suggesting it is a multidimensional phenomenon consisting of different cognitive and motivational processes. Evidence from different approaches — from task-based correlational neuroimaging to causal brain stimulation and neural trait research — has revealed a significant overlap between neural circuits engaged in a variety of prosocial behaviors. These networks involve mentalizing and empathy ability, reward and valuation processing, as well as capacity for cognitive control. Importantly, these findings also suggest that prosocial decision-making results from a complex interaction between individual characteristics and external influences. For example, among individuals with high mentalizing abilities expressed by high TPJ activation who are generally more prone to make prosocial choices, only those with high dlPFC activation tend to strategically align their behavior with contextual factors, such as rules, potential sanctions, or the behavior of others [9, 32, 37, 38].

Despite these fruitful insights, however, a full understanding of the complexity of human prosociality remains elusive. One promising avenue for future research may be the combination of different neuroscientific methodologies and other process tracing methods. For example, combining offline task-independent neural traits with online neural activation within the same sample of participants could provide more insights into the interplay of brain structure and function, yielding a clearer understanding of what functional or structural aspects of brain regions ultimately drive prosocial behavior. Moreover, a combination of online and/or offline neuroimaging with brain stimulation might allow researchers to localize cortical areas and characterize the baseline level of neural activation, which then allows a more precise investigation of trait-state interactions. Finally, these approaches might also benefit from the further integration of process tracing methods such as eye- and mouse-tracking, reaction time measures, or computational modeling [46, 47]. In addition to combining different methodologies, future research could also try to integrate tasks embedded in more natural contexts and across more diverse settings. For example, researchers could investigate whether neural mechanisms underlying prosocial choices differ when these choices are reached collectively as a group [48] or when they are made toward future generations [49–51]. By combining theoretical and methodological advances, we believe that future research will help us refine our previous knowledge and

generate novel insights into the mechanisms underlying prosocial decision-making.

Finally, we would like to add that every act of prosocial behavior is preceded and accompanied by multiple layers of processes that are utterly intertwined, such as chemical processes in the brain, hormones, genes, sensory cues, and other environmental influences. Neuroscience is just one of many disciplines that helps us gain a fuller understanding of the complex, multifaceted phenomena of prosociality. We believe that every discipline provides a novel perspective and contributes an additional layer of knowledge to our understanding of the factors that allow prosocial behavior to become apparent. What neuroscience contributes, in particular, are insights into the neural networks and neural processes that influence why, how, and when humans behave prosocially — including processes that are sometimes beyond conscious awareness or are hard to measure in an ‘objective’ manner (as opposed to self-report measures, for example). However, we would like to highlight that no discipline is *per se* superior to others but that they can complement one another in several ways and jointly contribute to a more comprehensive understanding of prosociality.

Conflict of interest statement

Nothing declared.

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