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A comparative fMRI meta-analysis of altruistic and strategic decisions to give

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The decision to share resources is fundamental for cohesive societies. Humans can be motivated to give for many reasons. Some generosity incurs a definite cost, with no extrinsic reward to the act, but instead provides intrinsic satisfaction (labelled here as 'altruistic' giving). Other giving behaviours are done with the prospect of improving one's own situation via reciprocity, reputation, or public good (labelled here as 'strategic' giving). These contexts differ in the source, certainty, and timing of rewards as well as the inferences made about others' mental states. We executed a combined statistical map and coordinate-based fMRI meta-analysis of decisions to give (36 studies, 1150 participants). Methods included a novel approach for accommodating variable signal dropout between studies in meta-analysis. Results reveal consistent, cross-paradigm neural correlates of each decision type, commonalities, and informative differences. Relative to being selfish, altruistic and strategic giving activate overlapping reward networks. However, strategic decisions showed greater activity in striatal regions than altruistic choices. Altruistic giving, more than strategic, activated subgenual anterior cingulate cortex (sgACC). Ventromedial prefrontal cortex (vmPFC) is consistently involved during generous decisions and processing across a posterior to anterior axis differentiates the altruistic/strategic context. Posterior vmPFC was preferentially recruited during altruistic decisions. Regions of the 'social brain' showed distinct patterns of activity between choice types, reflecting the different use of theory of mind in the two contexts. We provide the consistent neural correlates of decisions to give, and show that many will depend on the source of incentives.

1. Introduction

The decision to share resources is a cornerstone of any cooperative society. The motivations that drive these choices, however, will vary. Giving can be driven by intrinsic rewards, such as conditioned satisfaction from performing a generous act or the image of oneself as a 'good person'. On the other hand, giving can also be driven by strategic forethought of extrinsic rewards that might be gained through reciprocity, avoidance of punishment, or a public good. Some may argue that 'why' we give does not matter, as long as we do. However, understanding the 'why' is essential for determining the likelihood of prosocial behaviour in the absence of extrinsic benefit, such as when the beneficiary could never return the favour or when societies, which depend on prosocial behaviour, do not provide defined incentives. It can also help us understand how intrinsic and extrinsic drives interact in the decision process.

Over a decade of innovative neuroimaging studies have provided a fresh window into the old problem of why we give. Through this lens, we can see whether different motivations to help one another use different neural (and therefore cognitive) mechanisms. This then provides the basis for studying how these neurocognitive mechanisms may vary independently between contexts and individuals. This insight could also help to explain other phenomena. For instance, overlapping anatomy of intrinsic and extrinsic drives could underpin the effect of extrinsic incentives 'crowding out' altruistic motivations (Frey and Oberholzer-Gee, 1997), or make clear how intrinsic and extrinsic benefits sum in strategic decisions to help each other.

However, no systematic meta-analysis has examined the consistency of these findings on prosocial decision-making (see Filkowski et al., 2016 and Luo, 2018 for descriptive reviews, Gabay et al., 2014 for neuroimaging meta-analysis of ultimatum game responders and Bellucci et al.,

Abbreviations: ACC, Anterior cingulate cortex; AES:SDM, Anisotropic effect size signed differential mapping; AI, Anterior insula; dlPFC | dmPFC, Dorsolateral | Dorsomedial prefrontal cortex; fMRI, Functional magnetic resonance imaging; NuAcc, nucleus accumbens; OFC, Orbitofrontal cortex; PFC, Prefrontal cortex; PCC, Posterior cingulate cortex; ROI, Region of interest; sgACC, Subgenual anterior cingulate cortex; STS, Superior temporal sulcus; TPJ, Temporoparietal junction; vlPFC | vmPFC, Ventrolateral | Ventromedial prefrontal cortex.

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2017 for trust games). With this meta-analysis, we investigated the consistent neural correlates of decisions to give and differences in these correlates that depend on whether there is potential for extrinsic gain through the interaction.

We define *altruistic* choices to give as generous acts with no opportunity to gain extrinsic rewards as a direct result of that interaction. Motivations for giving in these contexts rely on intrinsic rewards. Sources of intrinsic reward or 'warm glow' (Andreoni, 1990, 1989) can include vicarious reward experience (Mobbs et al., 2009); relief of empathic concern (FeldmanHall et al., 2015); self-enhancement from adherence to moral codes or social norms (Niemi et al., 2017); and conditioned reinforcement (e.g. from parental feedback). Warm glow could also result from inferences of enhanced reputation (Izuma et al., 2010) in the eyes of an experimenter or omniscient religious figure, despite no defined benefit of that enhanced reputation. Intrinsic incentives to give are often studied with dictator games (Kahneman et al., 1986), donations to charities, or payments to prevent others from coming to harm (Table 1).

We define *strategic* choices to give as generous acts that might increase the probability of a defined extrinsic reward. Strategic choices can involve the intrinsic rewards of altruistic choices (Capraro, 2017), but add the possibility of extrinsic gain, which is thought to be the dominant weight in the decision process (Frey and Oberholzer-Gee, 1997). Extrinsic benefits could come through avoiding punishment (Fehr and Gächter, 2002); reciprocity of the recipient (Falk and Fischbacher, 2006; Fehr et al., 2002); collective contributions to a public good (Chaudhuri, 2011); enhanced gains from cooperation (Fehr and Fischbacher, 2004) or rewards from defined future interactions through having an enhanced reputation (Milinski et al., 2001; Nowak and Sigmund, 2005). Paradigms used to study strategic giving (Table 1) include the ultimatum game (Güth et al., 1982); trust game (Berg et al., 1995); public goods game (Rapoport, 1987); prisoners' dilemma (Luce and Raiffa, 1957); and repeated versions of these games which include opportunities for reputation building.

For altruistic choices, goal-attainment based on most intrinsic incentives begins at the time of the action, without delay. As a result, most intrinsic rewards are relatively certain. Warm glow can be modulated, in part, by the gift's (delayed and uncertain) impact on the recipient, but for most paradigms (all those included here), the participant does not observe this impact. Strategic rewards, on the other hand, are weighted to the uncertain effects of the gift on extrinsic outcomes. In these cases, goal attainment comes after the action, when others respond. Keeping money (which we label 'selfish', as opposed to being 'prosocial' by giving, cooperating, or trusting) in a strategic context enhances certainty and immediacy of reward, but could also lead to less money. In the altruistic context, a selfish choice does not change outcome certainty to the same degree, and will always leave the participant with more money.

Table 1
Explanation and categorisation of tasks used in studies.

Task	Description	Group
Dictator game	Participant either chooses an amount of their money to give or accepts/rejects a proposed split between themselves and the other player.	Altruistic
Charity donation task	Participant either chooses an amount of their money to donate or accepts/rejects a proposed split between the participant and a charity.	Altruistic
Pain vs. gain	Participant can give up varying amounts of money, the more given the less painful the electric shock given to a partner	Altruistic
Ultimatum game	Participant proposes a split between themselves and their partner that is only implemented if the partner accepts it.	Strategic
Trust game	Participant transfers an amount of money to the trustee that is multiplied by some factor (often 3). The trustee then chooses an amount to send back which decides the payoff for both players.	Strategic
Prisoner's dilemma	Participant and partner decide whether to cooperate or defect. They gain mutual benefit if both cooperate but individuals gain more by defecting if the partner cooperates.	Strategic
Public goods game	Participants invest an amount in a communal fund that is then multiplied and divided among all players, including those who did not initially contribute to the communal fund.	Strategic

The use of theory of mind – inferring others' mental states (Frith and Frith, 2006), also differs between altruistic and strategic decisions to give. In altruistic contexts, theory of mind is likely to be more weighted on how another will feel, rather than what they will do, considering appreciation, change of emotion, or disappointment of the other. This could occur via empathy processes (Lockwood et al., 2015) – feeling what the other is feeling (Decety et al., 2015), mentalising, or both, with variability across different people (Tusche et al., 2016). Assuming the inferred appreciation of a gift by the recipient would increase motivation to give, greater theory of mind is expected during altruistic decisions to give, relative to keeping the goods. Strategic decisions might balance that difference to a degree. Intention inferences can motivate either generous or selfish choices and therefore be equally associated with selfish and generous decisions.

In sum, both altruistic and strategic choices incur immediate costs that benefit others but differ in the sources, certainty, and immediacy of the associated reward. Theory of mind is likely to contribute to both decision types, but differently in each, with different dissociations between the prosocial and the selfish choice alternatives, see Fig. 1.

Two previous functional magnetic resonance imaging (fMRI) studies, which compared prosocial decisions in the altruistic dictator game with the strategic ultimatum game, report inconsistent findings and interpretations (Weiland et al., 2012; Zheng and Zhu, 2013). There was qualitatively no overlap of activation between them, creating concerns for the consistency and generalisability of reported differences. A third fMRI study using both ultimatum and dictator games to study childhood development of strategic social behaviour did not focus on the contrast between generous and selfish choices, but interestingly the difference in gift sizes between the two games (Steinbeis et al., 2012).

An fMRI meta-analysis integrates prior findings to increase the statistical power to detect reliable, consistent neural correlates of decision types (Müller et al., 2018; Wager et al., 2009, 2007). This is vital given that many fMRI reports are based on small sample sizes (Button et al., 2013; Cremers et al., 2017) and do not meet the new standards of high statistical thresholds recently shown to be required for confidence in effects (Eklund et al., 2016). In addition to the advantages associated with coordinate-based meta-analysis, our use of unthresholded maps enhances sensitivity (Radua and Mataix-Cols, 2012) and reduces assumptions of the spatial extent of activations. Our meta-analysis also allows new combinations and contrasts between different task types.

In this study, we do not make firm predictions of specific neural regions, remaining agnostic to previous findings as much as possible with a data-driven approach. One area that was identified as a region of interest *a priori*, however, was the ventromedial prefrontal cortex (vmPFC), as it is has been reliably linked to subjective value and decision-making (Bartra et al., 2013; Levy and Glimcher, 2012) including prosocial choices (Hare et al., 2010). It is also a large, cytoarchitecturally heterogeneous region (Mackey and Petrides, 2010) with varying connectivity (Sepulcre et al., 2010) and different sources of value show different activity patterns across it (Campbell-Meiklejohn et al., 2016; Sescousse et al., 2013). We therefore looked at activation across this region in more detail than the rest of the brain.

The present meta-analysis aims to answer four basic questions across the whole brain, with added focus on vmPFC:

i) What is common to altruistic and strategic decisions to give?
ii) What is consistent about altruistic decisions?
iii) What is consistent about strategic decisions?
iv) How do altruistic and strategic decisions differ?

There are examples of real-world decisions that do not fit into our

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