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Cutler, Jo; Campbell-Meiklejohn, D

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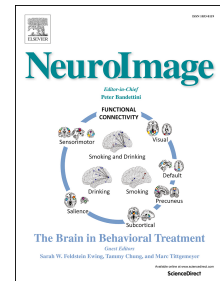
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Supplementary data related to this article can be found at https://doi.org/10.1016/j.neuroimage.2018.09.009.

Details of peaks (as well as statistical maps) can also be downloaded: https://doi.org/10.25377/sussex.c.4155923.

Analysis code, spreadsheet and demo data to adjust fixed, random and mixed effects fMRI meta-analysis to account for variable dropout between studies can be found here: https://doi.org/10.25377/sussex.c.4223411

Altruistic > selfish   Prosocial > selfish   Strategic > selfish

x = 0   x = 0   x = 2

n = 21   n = 36   n = 15

n = 36   Altruistic > strategic   Strategic > altruistic

Prosocial decisions across ventromedial prefrontal cortex

Mean effect size (Hedge's g)

- Altruistic
- Strategic

Posterior to anterior axis (voxels 1-20)

Voxel 1: x = 4, y = 30, z = -20; voxel 20: x = 4, y = 68, z = 10
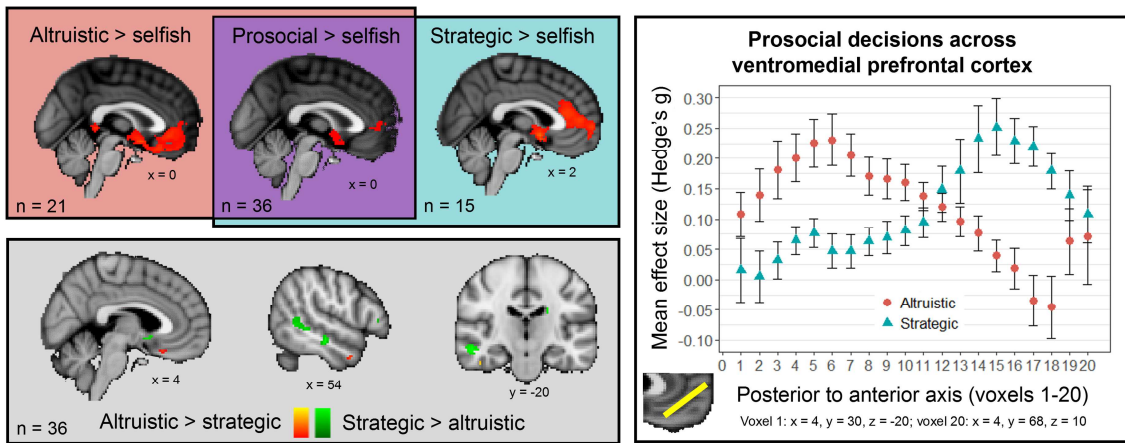
A comparative fMRI meta-analysis of altruistic and strategic decisions to give

Jo Cutler [a] and Daniel Campbell-Meiklejohn [a]

[a] School of Psychology, Pevensey Building, the University of Sussex, Falmer, BN1 9QH, UK.

Correspondence should be addressed to Dr. Daniel Campbell-Meiklejohn, School of Psychology, Pevensey Building, the University of Sussex, Falmer, BN1 9QH, UK.

E-mail: daniel.cm@sussex.ac.uk

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.

Abbreviations:

ACC: anterior cingulate cortex, AES:SDM: Anisotropic Effect Size Signed Differential Mapping, AI: anterior insula, dlPFC l dmPFC: dorsolateral l 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 l vmPFC: ventrolateral l ventromedial prefrontal cortex

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., 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.

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

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.

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.
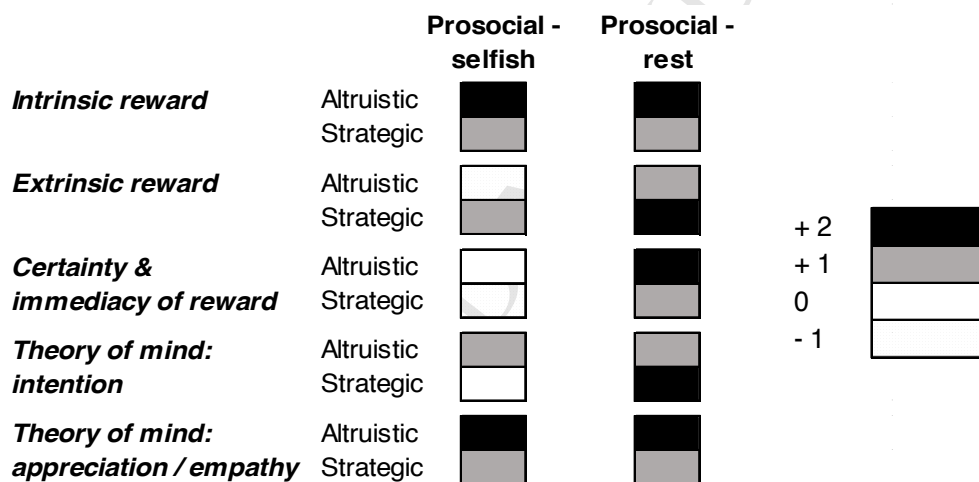
Figure 1. Theoretical presence in altruistic and strategic decisions to give compared to a selfish choice and to rest. This can act as a rough roadmap for interpreting neural differences between the two types of decision to give as well as each decision with the common controls used.

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 Figure 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 of 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 defined groups, such as tax deductions from charitable giving or defined payments for blood donation. We also do not cover outcomes of decisions such learning a person appreciated a gift or rewards associated with choosing a winning strategy. The scope of this meta-analysis is fMRI paradigms for which the data at the point of a decision is available. By better understanding the neural basis of altruistic and strategic decisions as defined here, we provide a foundation for investigations in other contexts, as well as a milestone for research over the last fifteen years.

2. Method

2.1. Literature search and study selection

Literature searches using PubMed and Web of Science identified research added before September 2016. Keywords were either "fMRI" or "neur*" as well as one of: "altruis*", "charity", "charitable", "prosocial", "cooperation", "public goods", "social value orientation", "reputation",

"dictator", "ultimatum", "trust game", "prisoner*". We identified additional potential articles from reference lists of selected articles or those offered by authors (Figure 2). Articles were considered if they reported novel fMRI data, not reported elsewhere, collected while participants made decisions, and analysed whole-brain data. For studies that either used psychopharmacological manipulations or tested populations other than healthy participants, we requested data from just the control group.

In addition, studies were screened for eligibility for the two groupings. Decisions in the altruistic group were defined as decisions that benefitted at least one other person at a cost to the self, with no potential for an extrinsic benefit. Paradigms were dictator games, pain vs gain or donation tasks. Decisions in the strategic group benefitted at least one other person but could also benefit the decision-maker. Common paradigms included trust and ultimatum games. Almost all selected studies focused on deciders rather than responders in these games. Responders, who may be prosocial due to reciprocity norms, have been studied previously (Gabay et al., 2014). One study (Garbarini et al., 2014) only had data from the responder role in a trust game but with a clear incentive for participants to build up a prosocial and trustworthy reputation in order to receive future investments. All participants thought partners were human, which was true in some cases but not others. For all studies, the data were from the decision phase of the task.

Overall, we identified 35 altruistic and 45 strategic fMRI studies and requested statistical maps from the authors. Due to substantial methodological variation across studies, letters requested the decision of interest contrasted with as many as possible of a high-level control, baseline of some kind and the selfish choice. Obtaining multiple maps for a study maximised the likelihood of similarities between studies and shows whether specific contrasts affected results. If maps were not available, we requested coordinates for contrasts of interests or extracted them from manuscripts. Of these, a coordinate-based analysis was available for eight studies, while others did not report the required contrasts in manuscripts.

Of 35 altruistic studies, 18 authors provided usable maps (51% response rate) and three had coordinates, resulting in data from 557 participants in this group. Of 45 strategic studies, 10 authors provided maps (22%) and five had coordinates, giving data from 593 participants in this group.

2.2. Analysis

A combined image and coordinate-based meta-analysis of retrieved data was conducted using Anisotropic Effect Size Signed Differential Mapping software (AES:SDM, Version 4.31; Radua et al., 2014). When available, statistical maps enhance the sensitivity of the analysis and allow incorporation of both positive and negative differences. With coordinates, the software recreates estimated statistical maps from coordinates and their effect sizes using an anisotropic kernel. If the contrast of interest was available in both directions (e.g. cooperate > defect and defect > cooperate), the opposite peaks became negative t-values. The incorporation of study sample size increases the weight of larger studies.

A random-effects model, using the recommended 50 permutations, implemented all maps. This creates 50 random models with the same number of foci as the map of interest and

tests the null hypothesis that the map's activations are the result of random distribution throughout the brain. Thresholding parameters used were those recommended by Radua et al. (2012) who found a voxel-level threshold of $p<0.005$ to approximate $p<0.05$ corrected and optimally balance specificity and sensitivity. Reported z-scores are specified as SDM-Z as they do not follow a standard normal distribution.

2.3. Contrasts and covariate

The available datasets used a range of control conditions broadly classified as rest (including one-sample tests), visuomotor controls, or selfish decisions. These controls vary significantly across multiple processes so we used an overall covariate in our models that codes for *comparator complexity* to control for differences, rating control conditions from 1 to 4 (see Supplementary Materials S1.2. for details).

For separate analyses of altruistic and strategic decisions, variance attributed to complexity was used to model contrasts between prosocial (generous) decisions and rest (a contrast where the covariate is at its modelled minimum) and between prosocial and selfish decisions (where the effect of the covariate is at its modelled maximum). By including the covariate in the model, we aimed to allow specificity in our interpretations of activity while maintaining statistical power (by including all available data). In addition, we specifically contrasted prosocial choices to the selfish alternative, only in the studies that had this comparison. This enabled tests of robustness that require a relatively homogenous group (see Supplementary Materials for details S1.3. and results S2.1.1.).

We used SPM12 (Statistical Parametric Mapping, http://www.fil.ion.ucl.ac.uk/spm) to extract areas of overlapping activation common to altruistic and strategic decisions, for example areas significant in both the altruistic > selfish and strategic > selfish maps. These maps were those from the overall analyses described above which use the comparator complexity covariate to model contrasts with rest and selfish decisions while incorporating all studies.

Differences between the decision types were calculated in both directions (altruistic > strategic and strategic > altruistic) using linear models in AES:SDM. For these comparisons, we entered comparator complexity as a covariate of no interest. Comparisons and overlap were also tested in the subgroup of studies with a selfish control.

2.4. Labels and atlases

As AES:SDM uses a white matter template for labels, these were converted to grey matter labels with the Harvard-Oxford atlas in FSL (FMRIB Software Library, www.fmrib.ox.ac.uk/fsl). We also labelled regions according to labels used in relevant literature. The temporoparietal junction (TPJ), posterior superior temporal sulcus (pSTS), dorsolateral prefrontal cortex (dlPFC), ventrolateral PFC (vlPFC) and dorsomedial PFC (dmPFC), coordinates were used from the *a priori* regions of interest constructed by Telzer et al. (2011). However, we refer to their medial PFC here as the vmPFC and extend this region further ventral and posterior compared to the boundaries of that paper for our ROIs (see below). We also used connectivity-based parcellation atlases in FSL for further subdivision of the dorsal PFC (Sallet et al., 2013) and medial PFC and cingulate (Neubert et al., 2015).
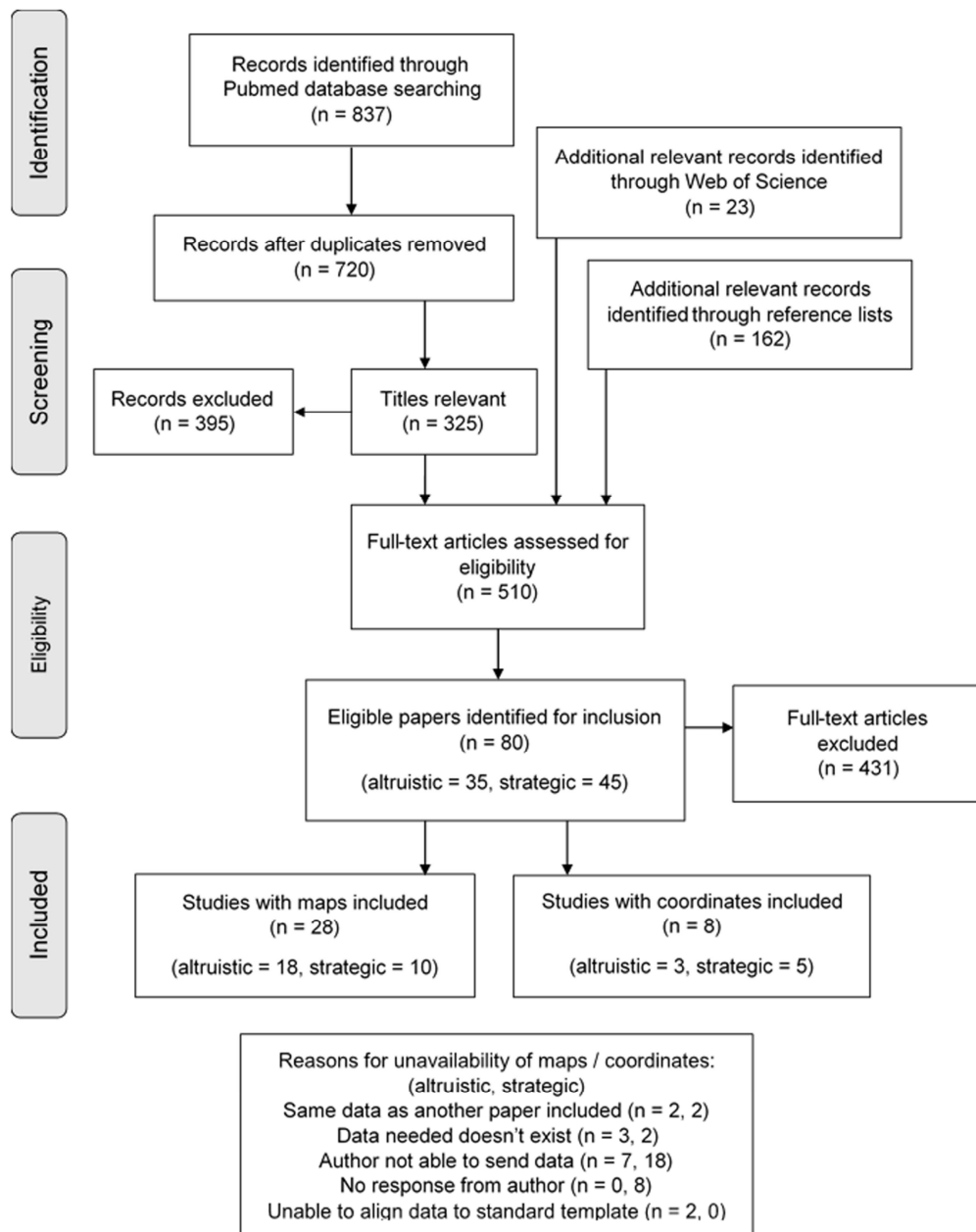
Figure 2. Flow diagram of studies included and excluded at each stage of identification and verification following PRISMA guidelines (Moher et al., 2009).

2.5. ROI Analysis

To test the prediction that different types of prosocial decision may show different patterns of activation across the heterogenous vmPFC, values were extracted from across an anatomical axis. These regions were defined *a priori* by spheres used previously (Campbell-Meiklejohn et al., 2016) and similar to methods used in recent studies (De Martino et al., 2017; Nicolle et al., 2012; Sul et al., 2015; Yankouskaya et al., 2017). Effect sizes were extracted from single voxels along the same axis for our analysis (see details in Supplementary Materials S1.4. & Figure 8).

2.6. Accounting for dropout

A key region of interest, the vmPFC, is known to suffer from distortion and dropout during fMRI scanning due to factors including proximity to air and bone around the sinuses (Ojemann et al., 1997). While techniques have been developed to minimise this (Weiskopf et al., 2007) they are not universally employed and the inclusion of older studies in the meta-analysis meant that the coverage needed to be examined. This was done by binarising each map, after registration to a common template, based on whether there was signal in each voxel or not and summing these images to create coverage maps (Figure 3).
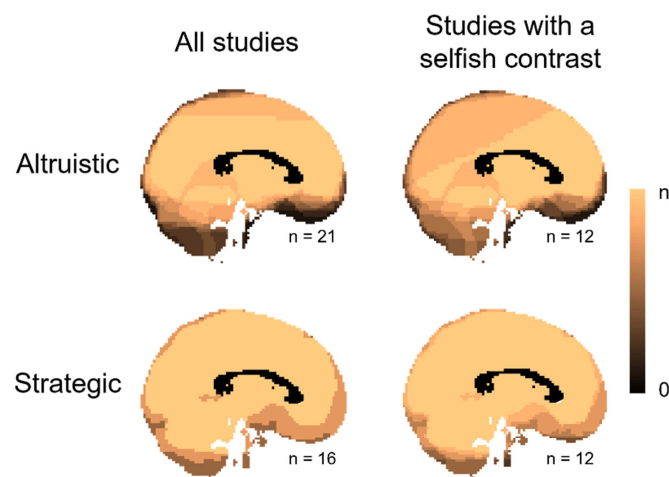
Figure 3. Coverage maps showing the number of studies with data in each region, x = 0, n = the number of studies available and the maximum possible coverage.

These maps show a decline in coverage around the anterior and inferior edge of the vmPFC, particularly for altruistic studies. With missing data represented as values of 0, this lack of coverage risked false negatives in reported results. To overcome this, we ran an *adjusted analysis* by modifying the calculations run by AES:SDM using SPM12 to only include studies with data present, on a voxel by voxel basis (see details in Supplementary Materials S1.5.). We did this only on the subgroup of studies with a contrast with selfish decisions.

Table 2.

Details of studies included in the meta-analysis

First author	Date	tN	F	N	Map or peaks	T	FWHM (mm)	Program	Sig	Contrast selected	Definition & additional info	Control / code
The focus of the study								The method used in the study				
Altruistic group												
Hare	2010	22	22/22	22	Map	3T	8	SPM5	<.05 C	PM by amount given	Free trials only	S / 4
Social value computations												
Izuma	2010	29	12/23	23	Map	3T	6	SPM5	<.001 U	Donation vs fixation	Only when not observed	R / 1
Effect of an observer										Accept or decline the same payoff each time to a charity		
Telzer	2011	25	13/25	25	Map	3T	8	SPM5	<.05 FDR	Costly donation vs fixation	Across ethnicity	R / 1
Whether self-control and mentalising activation when giving to family and if moderated by family obligation										Accept or decline proposed payoff to self and family - costly / non-costly reward / donation		
Brosch	2011	19	11/19	19	Map	3T	8	SPM8	<.05 FWE	Costly donation vs control	Control = self and charity -1	V / 3
Self-interest and openness to change values										Accept or decline proposed payoff to self and charity - reward, (non)costly donation, control		
FeldmanHall	2012	20	8/14	14	Peaks	3T	8	SPM	<.001 U	PM by amount given (+) and amount kept (-)	Only in real decisions	S / 4
Real vs hypothetical moral decisions										Real and imagined pain vs gain task		
Morishima	2012	30	17/30	27	Map	/	8	SPM8	<.05 FWE	Donation vs selfish		S / 4
Whether altruism correlates with TPJ structure and function										Choose between 2 proposed payoffs for self and other - advantageous or disadvantageous inequality		
Gunther Moor	2012	53	31/53	49	Map	3T	8	SPM5	<.001 U	Generous vs fixation	Across ages (22 age 10-12, 16 age 14-16, 15 age 19-21)	R / 1
Developmental differences in dictator game after										Dictator allocations to people who included or excluded participants during previous cyberball		

Study	Year	N	exclusion	n	Localization	Field	Smoothing	Software	p	Correction	Contrast	Notes	Rating
Lelieveld	2012	26	17/26	18	Map	3T	6	SPM5	<.001	U	Prosocial decision vs selfish	Data doesn't separate response from decision	S / 4
Effect of receiver's emotional reaction											Participants who split 6-4 in dictator game split again after emotional feedback from receivers		
Genevsky	2013	30	14/22	22	Peaks	3T	4	AFNI	<.05	C	Donation vs not donating	Across conditions	S / 4
Neural basis of identifiable victim effect											Accept or reject requested donation to children with varying information (name, photo) available		
Kuss	2013	33	17/33	33	Map	3T	6	SPM8	<.001	U	Costly donation vs pure self-interest	Control: self-interest choices	V / 3
Motivation for donating using reward prediction error											Choose between 2 proposed payoffs for self and other – (non)costly donations, self-interest or efficiency		
Guroglu	2014	28	17/28	22	Map	3T	8	SPM8	<.001	U	Generous vs selfish		S / 4
Activations linked to inequity, regardless of benefactor											Choose between 2 proposed payoffs for self and other – fair or unequal benefitting either self or other		
Pulcu	2014	15	9/15	14	Map	3T	5	SPM8	<.05	FWE	Generous vs control	Healthy controls only, control: no gains	V / 3
Altruism activity in remitted major depressive disorder											Accept or decline proposed payoff to self and charity – (non)costly donations, both gain, P gains, no gains		
Koban	2014	22	10/22	17	Map	3T	8	SPM8	<.001	U	Sharing vs keeping	Human partner, conflict trials	S / 4
Activity related to interpersonal conflict for resources											Participant to share or keep resources when they and another player chose the same token (conflict)		
FeldmanHall	2015	19	11/17	17	Peaks	3T	8	SPM5	<.001	U	PM by amount kept (-)	With no covariates	S / 4
Personal distress vs empathic concern explanations											Pain vs gain task		
Hutcherson	2015	61	0/61	51	Map	3T	8	SPM5	<.05	FWE	Prosocial decision vs selfish	Decisions always created a selfish and a prosocial choice	S / 4
Propose and test a model of altruistic choice											Accept and rate 1-4 (strong no, no, yes, strong yes) split between self and other, 40% decisions reversed		
Strombach	2015	27	13/27	23	Map	3T	8	SPM8	<.005	U	Generous vs selfish	Across social distances	S / 4
Effect of social distance on prosocial decision activity											Choose between 2 proposed payoffs for self and other (diff social distances) - one selfish and		

Author	Year		Ratio		Type	Scanner	N	Software	Threshold	Contrast	Across	Cat.
Telzer	2015	29	13/29	26	Map	3T	8	SPM8	<.05 FWE	Generous vs fixation	Across recipients	R / 1
											one generous	

Cultural differences in ingroup and outgroup helping — Choose between 2 proposals for self or other - ingroup donations, outgroup donations and pure reward

Author	Year		Ratio		Type	Scanner	N	Software	Threshold	Contrast	Across	Cat.
Will	2015	28	16/26	26	Map	3T	8	SPM5	<.001 U	Generous vs fixation	Across includes and excluders	R / 1

Correlates of punishment and forgiveness after exclusion — Dictator allocations to people who included or excluded participants during previous cyberball game

Author	Year		Ratio		Type	Scanner	N	Software	Threshold	Contrast	Across	Cat.
Kuss	2015	40	22/40	36	Map	1.5T	8	SPM	<.05 FWE	Costly donation vs control	Across prosocials and proselfs, control: both benefit	V / 3

Impact of social value orientation individual differences — Choose between 2 proposed payoffs for self and other – (non)costly donations, self-interest or efficiency

Author	Year		Ratio		Type	Scanner	N	Software	Threshold	Contrast	Across	Cat.
Tusche	2016	33	15/33	32	Map	3T	8	SPM8	<.05 FWE	High vs low donations	Scale $0-$50, 'selfish' = lowest ½ donations	S / 4

Differences in neural patterns for different giving motives — Decide on a scale how much to donate to a charity

Author	Year		Ratio		Type	Scanner	N	Software	Threshold	Contrast	Across	Cat.
Will	2016	46	28/46	46	Map	3T	8	SPM8	<.001 U	Costly prosocial vs selfish	Across stable and rejected	S / 4

Sharing activity in chronically rejected and stable adolescents — Choose between 2 proposed payoffs for self and other in costly, non-costly and envious conditions — Equitable or inequitable payoff for self and other

Strategic group

Author	Year		Ratio		Type	Scanner	N	Software	Threshold	Contrast	Across	Cat.
Delgado	2005	14	6/14	12	Peaks	3T	4	Brain Voyager	<.001 U	Trust vs defect	Across reputations	S / 4

Effect of responder's responses and reputation — Repeated trust game after reading description of responder and getting feedback on their decisions

Author	Year		Ratio		Type	Scanner	N	Software	Threshold	Contrast	Across	Cat.
Krueger	2007	44	22/44	44	Peaks	3T	8	Brain Voyager	<.005 U	Trust vs control	Control similar to trust game	V / 3

Neural mechanisms of building trust

Alternating non-anonymous multi-round trust game

Author	Year	N	M/F	Type	Scanner	#	Software	Threshold	Contrast	Notes	Code
Sharp	2011	10	0/10	Map	3T	4	AFNI	<.001 U	Trust vs keep / rest	Healthy controls only, across partners	S&R / 4&1

Reputation and reward processing in young boys with externalising behaviour problems

| Fareri | 2012 | 25 | 9/18 | Map | 3T | 8 | Brain Voyager | <.001 U | Cooperate vs control / one sample | Used data from both participants as alternated roles, control: lottery | V&R / 3&1 |

Effect of being excluded

Trust game after being excluded or not by different players

| Stanley | 2012 | 51 | 22/40 | Peaks | 3T | 6 | SPM8 | <.05 C | PM by amount sent | Human only, across exclusion | S / 4 |

Effect of race as a reputation proxy on trust

Trust game with people of different races

| Fouragnan | 2013 | 20 | 0/20 | Peaks | 4T | 18 | SPM8 | <.05 FWE | Trust vs keep | Across partners | S / 4 |

Effect of reputation on response to trust violations

Trust game with cooperative and individualistic partners with a reputation for being one or the other

| Smith-Collins | 2013 | 27 | 27/27 | Peaks | 1.5T | 24 | SPM8 | <.001 U | Cooperate vs control / defect | Across races, control: remembering faces | S&V / 4&2 |

How brain updates representations of partners to learn

Two round trust game with the same players, receiving feedback on trustworthiness after first

| Bault | 2014 | 29 | 12/29 | Map | 3T | 5 | FSL | <.05 FWE | PM by amount sent | Across social distances | S / 4 |

Dynamic model of social tie development

Repeated public goods game with the same partner

| Emonds | 2014 | 38 | 22/38 | Map | 3T | 4 | Brain Voyager | <.01 U | Cooperate vs defect | Across ethnicity and group given to | S / 4 |

Differences between prosocials and proselfs in neural activity and impact of trust

Prisoner's dilemma game with measure of SVO and dispositional trust

Study	Year	tN	F	N	Map/Peaks	T	Brain software	FWHM	sig	Contrast	Control / Notes	Aim	Task	Code
Garbarini	2014	16	8/16	16	Map	1.5T	Brain Voyager	4	<.05 C	Giving back vs not / rest	Used trustee data due to reputational manipulation	Gender differences in reputation building	Act as trustees in trust game with either reputation being monitored or not	S&R / 4&1
Fett	2014	45	0/45	45	Map	3T	XBAM	8.8		Trust vs control	Control: put cursor to target	Modulation of mentalising by attachment style	Prisoner's dilemma game with measures of attachment style	V / 2
Ramsøy	2015	14	11/14	14	Peaks	3T	SPM8	8	<.05 FWE	Cooperate vs defect	Across frames	Role of empathy as a heuristic in decision making	Iterated prisoner's dilemma game framed as competition or cooperation with trait empathy measures	S / 4
Schneider-Hassloff	2015	16 / 4	78 / 164	16 / 4	Map	3T	SPM8	8	<.001 U	Cooperate vs control / defect	Control: "#" appeared in matrix – no points or partner	Modulation of mentalising by attachment style	Prisoner's dilemma game with measures of attachment style	S&V / 4&2
Chen	2016	10 / 4	50 / 10	93 / 4	Map	3T	FSL	5	<.05 FWE	Cooperate vs defect	Only placebo group with humans	Oxytocin & vasopressin effects during cooperation	Iterated prisoner's dilemma following administration with human or computer partner (total N = 304)	S / 4
Fermin	2016	41	18/33	33	Map	3T	SPM8	8	<.005 U	Cooperate vs one sample / defect	Across prosocials and proselfs	Differences between prosocials and proselfs in structure and function	Prisoner's dilemma with measures of SVO	S&R / 4&1

Note. tN = total sample in study, N = sample used in study, F = number of female participants as a fraction of tN or N depending on information provided, T = field strength of scanner in tesla, FWHM = full width half maximum size of smoothing kernel, sig = significance threshold used in study (this is relevant for studies with peaks but provided for those with maps to show peak thresholds are in line with other research), U = uncorrected for multiple comparisons, C = corrected for multiple comparisons, FWE = with family-wise error correction, FDR = with false discovery rate correction, PM = parametric modulation. Control: R = rest (including one sample t-tests), V = visuomotor control, S = selfish decision (including parametric modulation by generosity), Code = code for complexity of the control condition from 1 (minimum) to 4 (maximum).

3. Results

3.1. Mean analyses

3.1.1. Altruistic

Compared to being selfish, making a prosocial choice in an altruistic context showed significant activation in nucleus accumbens (NuAcc), subgenual (subcallosal) area of the anterior cingulate cortex (sgACC), vmPFC, orbitofrontal cortex (OFC), left dlPFC (Sallet et al., 2013 area 8B), pre-supplementary motor areas (pre-SMA), posterior cingulate cortex (PCC) and right cerebellum. Regions showing greater activation during selfish than altruistic decisions included bilateral dlPFC (areas 46 & 9), bilateral putamen, right caudate nucleus, bilateral posterior STS, bilateral frontal poles, and left amygdala (Figure 4a & Table 3).

Comparisons to 'rest' tell us how the brain is responding generally, in the decision context. These maps can be useful for making future predictions, but also aid the interpretation of the other contrasts. For instance, a region being 'more active' in one condition compared to another may counterintuitively actually reflect relatively less deactivation in that condition, relative to a common baseline.

Altruistic decisions contrasted with rest showed significant activation in ACC (Neubert et al. 2015 area 8m), right anterior insula (AI), bilateral dlPFC (area 46V), SMA and occipital cortex. Areas less active during the decision were vmPFC extending into left dmPFC, posterior insula, left precuneus, separate dlPFC regions (areas 8B & 46D), bilateral vlPFC, and temporal sulci, including TPJ and the pSTS in both hemispheres (Figure 4b & Supplementary Table 1).
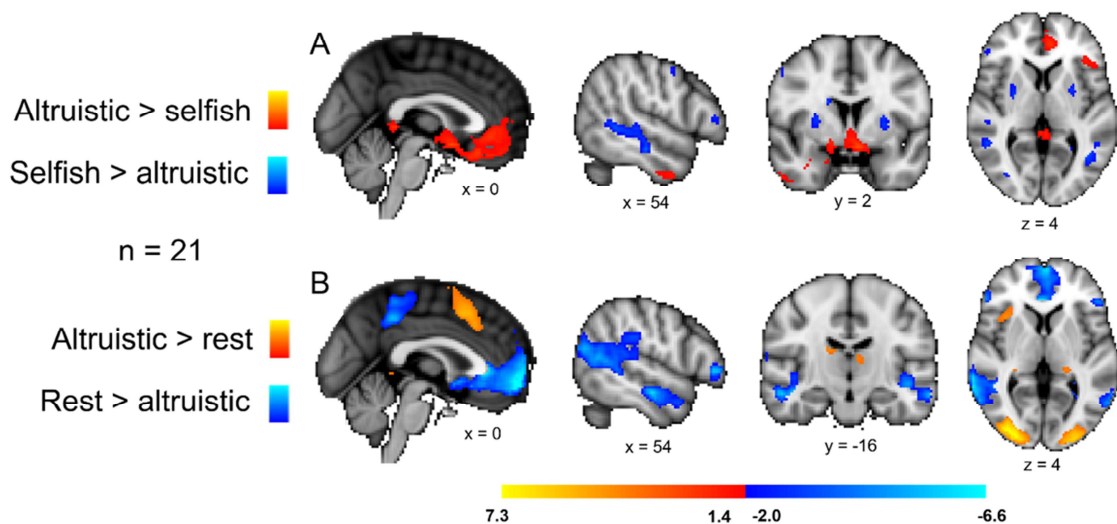
Figure 4. Mean activations from altruistic meta-analytic maps from modelled contrasts using the complexity covariate modelled **A:** at maximum – selfish control and **B:** at minimum – rest control (thresholded with permutation analysis run in AES:SDM). Coronal images in radiological orientation (right = left).

Table 3.

Peak activations from modelled contrasts using complexity coordinate for altruistic vs. selfish

| Peak label	BA*	coordinates			SDM-Z	Vox
		x	y	z		
Altruistic > selfish						
L striatum	25	-4	6	-12	3.38	1798
R orbitofrontal cortex	11	22	16	-20	2.81	360
R inferior temporal gyrus	20	44	-10	-36	2.37	158
L orbitofrontal cortex	11	-22	16	-22	2.61	97
Posterior cingulate gyrus		0	-38	2	2.39	92
L frontal operculum cortex	47	-40	28	4	1.96	67
L middle frontal gyrus	44	-54	24	30	2.04	65
L superior frontal gyrus		-16	34	44	1.72	46
L inferior temporal gyrus	37	-56	-56	-14	2.23	38
R parahippocampal gyrus		24	-14	-34	1.75	17
R cerebellum, crus II		46	-68	-42	1.67	16
R middle temporal gyrus	21	60	0	-18	1.67	13
L orbitofrontal cortex		-34	32	-8	1.85	12
R cerebellum, hemispheric lobule VI	37	34	-38	-34	1.71	12
R inferior temporal gyrus	20	60	-28	-24	1.85	10
Selfish > altruistic						
L supramarginal gyrus	22	-52	-46	14	3.38	526
R middle temporal gyrus		46	-34	-4	3.75	374
L temporal occipital fusiform cortex	19	-30	-62	-6	2.96	332
L frontal pole		-22	44	24	2.76	225
R putamen		26	-2	6	2.58	73
R caudate		18	-16	26	2.95	66
L putamen		-26	2	4	2.58	60
R inferior lateral occipital cortex		34	-72	12	3.08	57
R inferior frontal gyrus	45	50	34	6	2.53	29
L amygdala		-26	-10	-16	2.41	19
L superior lateral occipital cortex		-20	-78	18	2.43	17
R frontal pole		26	38	22	2.23	15
L precentral gyrus	6	-28	-12	54	2.32	11
L lingual gyrus		-26	-54	4	2.25	11
L precentral gyrus		-40	-10	40	2.37	10
L precentral gyrus		-50	-6	50	2.32	10
R precentral gyrus	6	54	0	46	2.41	10
R frontal pole	47	48	38	-6	2.17	10

Note. L = left, R = right, BA = Brodmann area, coordinates (x, y, z) in MNI space, SDM-Z= SDM z-value of activation, Vox = number of voxels in the cluster. *If cluster falls within *more* than one BA, none is reported either by AES:SDM software, or here.

3.1.2. Strategic

Strategic prosocial decisions, compared to selfish decisions, related to significantly higher activation in bilateral NuAcc, sgACC, vmPFC, ACC, right precuneus, right amygdala and regions of the cerebellum. Selfish strategic choices related to more activity in left TPJ, anterior middle temporal regions, right temporal pole and pre and postcentral gyri (Figure 5a & Table 4).

Compared to rest, strategic prosocial choices evoked similar results to altruistic prosocial choices in the equivalent analysis: activation in ACC (area 8m), bilateral AI, widespread bilateral dlPFC regions, SMA and occipital cortex. In addition, strategic decisions showed activation in bilateral putamen and the right caudate. Deactivation was across vmPFC, left dmPFC, bilateral posterior insula, bilateral precuneus, left dlPFC (area 8B), left vlPFC, bilateral TPJ and posterior & anterior STS regions (Figure 5b & Supplementary Table 2).
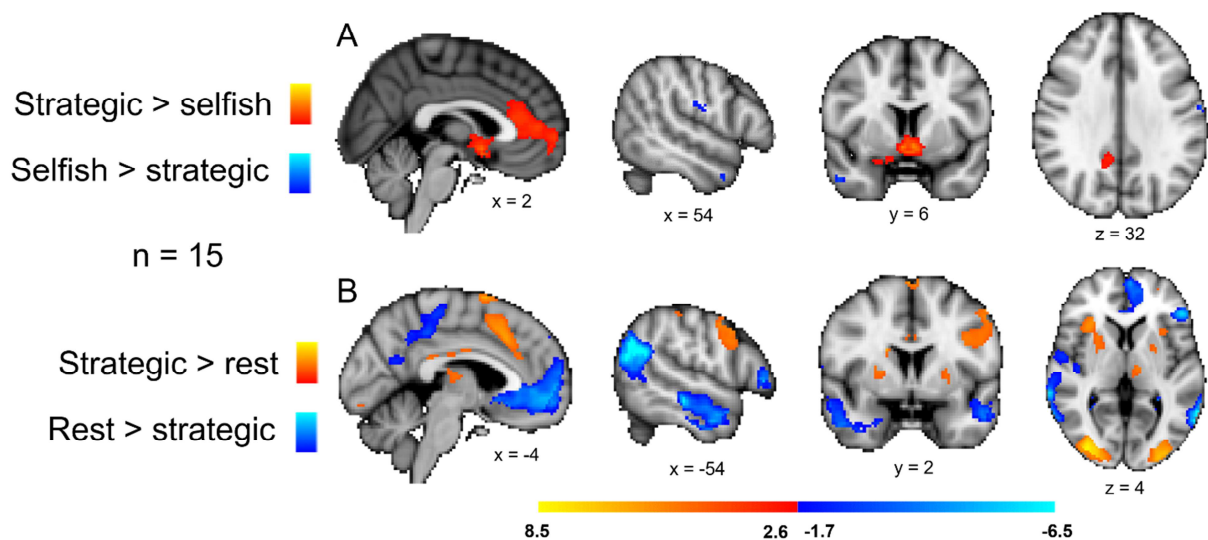
Figure 5. Mean activations from strategic meta-analytic maps from modelled contrasts using the complexity covariate modelled **A:** at maximum – selfish control and **B:** at minimum – rest control (thresholded with permutation analysis run in AES:SDM). Coronal images in radiological orientation (right = left).

Table 4.

Peak activations from modelled contrasts using complexity coordinate for strategic vs. selfish

Peak label	BA*	coordinates			SDM-Z	Vox
		x	y	z		
Strategic > selfish						
Paracingulate / anterior cingulate cortex		14	48	10	4.14	1017
L striatum		-6	2	-12	5.47	659
R precuneus cortex		12	-54	34	3.39	82
Cerebellum, vermic lobule VIII		18	-58	-42	4.45	26
R orbitofrontal cortex		22	28	-10	3.73	26
R amygdala		18	4	-18	3.11	26
Middle cerebellar peduncles		28	-46	-38	3.32	14
R superior lateral occipital cortex	39	42	-68	42	2.91	15
R cerebellum, crus I		28	-86	-28	3.19	11
L cerebellum, hemispheric lobule VIII		-14	-60	-44	3.12	11
R cerebellum, hemispheric lobule IX		6	-54	-46	2.96	10
Selfish > strategic						
R postcentral gyrus		54	-10	20	2.07	65
R temporal pole	21	52	6	-32	2.65	44
R brainstem		16	-28	18	3.03	41
R precentral gyrus		8	-20	56	2.09	36
L angular gyrus	39	-40	-56	22	2.63	32
R precentral gyrus		18	-12	60	2.51	29
L postcentral gyrus	43	-62	-8	32	2.47	13
L middle temporal gyrus	20	-58	-14	-28	2.06	12
R parietal operculum cortex		34	-22	20	1.84	10

Note. L = left, R = right, BA = Brodmann area, coordinates (x, y, z) in MNI space, SDM-Z= SDM z-value of activation, Vox = number of voxels in the cluster. *If cluster falls within *more* than one BA, none is reported either by AES:SDM software, or here.

3.2. Overlap

Overlaps were analysed using SPM to identify regions significant in both altruistic and strategic maps for a given contrast. These maps use the complexity covariate to model contrasts with rest and selfish decisions while incorporating all studies.

Compared to the selfish alternative, both types of prosocial choice showed overlapping activity in left NuAcc, ACC (sgACC and area 32), vmPFC and right OFC (Figure 6a). There was no overlap of areas responding more to the selfish choice (selfish > prosocial).

When contrasted with rest, altruistic and strategic decisions both activated bilateral ACC (area 8m), right AI, bilateral thalamus, bilateral SMA, pre-SMA, bilateral occipital and parietal cortices. Altruistic and strategic decisions showed overlapping deactivations in vmPFC, right temporal pole, left precuneus, left dlPFC (area 8B), right posterior insula, left OFC and bilateral TPJ & posterior STS (Figure 6b).
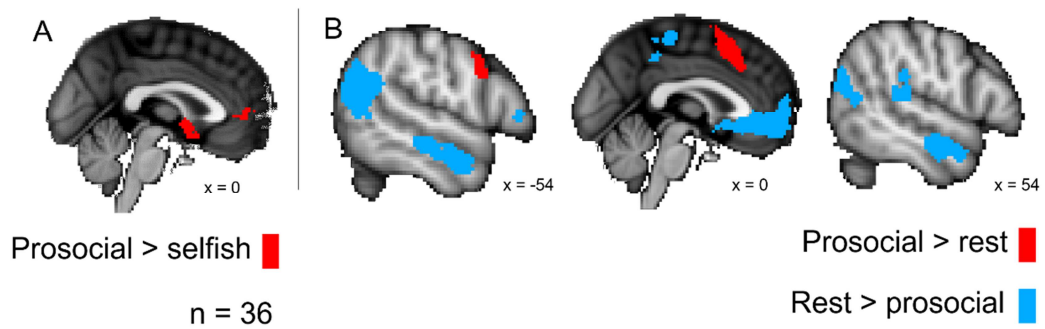
Figure 6. Overlap between altruistic and strategic decisions maps from modelled contrasts using the complexity covariate **A:** *vs.* selfish decisions and **B:** *vs.* rest.

3.3. Comparison

Areas more active during altruistic prosocial choices than strategic prosocial choices were the sgACC, left TPJ, left anterior STS, left inferior frontal gyrus, right temporal pole, right inferior temporal gyrus and bilateral thalamus. Strategic prosocial choices, compared to altruistic prosocial choices, showed more activity in the right NuAcc, left caudate, right dlPFC (area 46D), right posterior STS and right frontal pole (Figure 7 & Table 5).
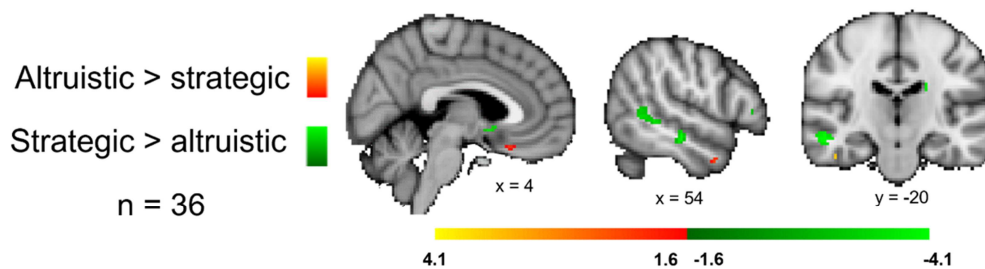
Figure 7. Comparisons between altruistic and strategic decisions controlling for complexity (thresholded with permutation analysis run in AES:SDM). Coronal image in radiological orientation (right = left).

Table 5.

Regions showing significantly greater activation in altruistic or strategic studies.

Peak label	BA*	coordinates			SDM-Z	Vox
		x	y	z		
Altruistic > strategic						
R temporal pole	21	52	6	-32	2.45	27
L angular gyrus	39	-40	-54	22	2.55	26
L inferior frontal gyrus		-40	32	2	2.40	21
L thalamus		-14	-28	18	2.79	14
Subcallosal cortex	11	4	22	-20	2.10	15
R thalamus		16	-28	18	2.37	12
L middle temporal gyrus	21	-66	-30	-4	2.25	12
R inferior temporal gyrus	20	46	-18	-30	2.57	10
Strategic > altruistic						
R middle temporal gyrus		52	-38	-4	3.98	110
R inferior frontal gyrus	45	50	34	6	3.42	76
R middle temporal gyrus		52	-22	-16	4.23	49
R striatum	25	4	6	-8	3.72	13
R frontal pole	46	30	44	34	3.17	13
L caudate		-20	-18	24	3.56	10

Note. L = left, R = right, BA = Brodmann area, coordinates (x, y, z) in MNI space, SDM-Z= SDM z-value of activation, Vox = number of voxels in the cluster. *If cluster falls within *more* than one BA, none is reported either by AES:SDM software, or here. Activations are after controlling for the complexity of the control task.

3.4. ROI analysis

Previous findings have shown that trajectories across the vmPFC can delineate decision types. Values were examined at the same 20 y and z coordinates (see Supplementary Figure 1) for x = 0, x= 4 and x = -4. Results reported here are from x = 4 as this plane showed the most striking differentiation but results for x = 0 and x = -4 were similar (see Supplementary Materials S2.2. and Supplementary Figure 5).

We ran linear models on each study's extracted effect sizes for each voxel using (i) all the data, including zero values and (ii) only the studies with data in that voxel, on a voxel-by-voxel basis. In both cases, a mixed-effects model was a better fit than a fixed-effects model. Both analyses revealed an interaction between vmPFC voxel location and decision group, (i) $t(22)=3.11$, $p=.005$; (ii) $t(21.1)=3.31$, $p=.003$. Altruistic activation was greatest in posterior vmPFC, as suggested by the whole brain results, and decreased moving anterior, whilst strategic activation increased along this axis (Figure 8).
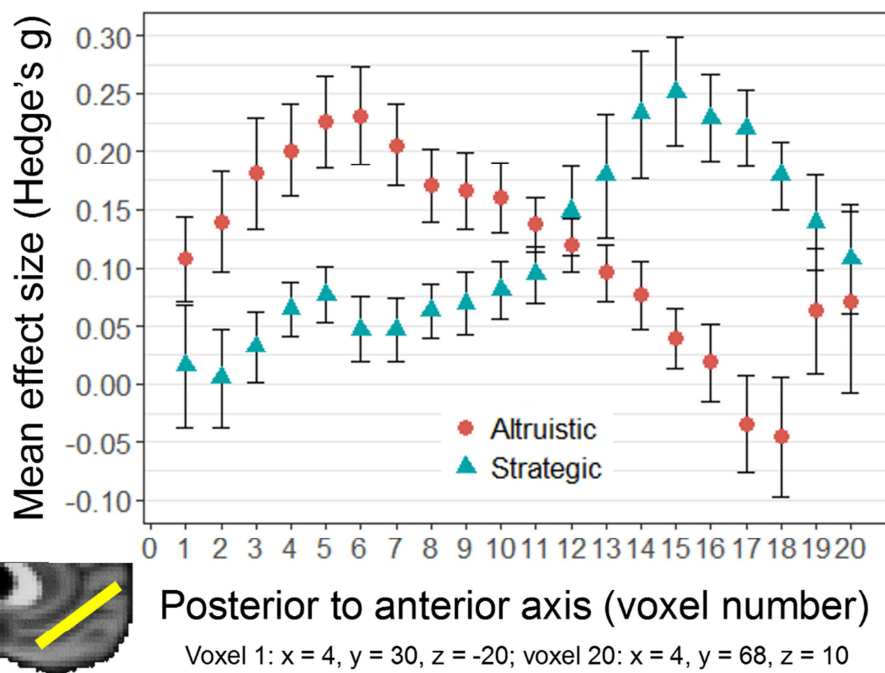
Figure 8. vmPFC ROI analysis: average effect sizes of activation for each group for each voxel at x = 4, not including studies with no data in that voxel (see Supplementary Figure 1 for exact location of voxels and Supplementary Figure 5 for graphs including all data). Error bars depict standard error.

3.5. Adjustment for dropout

As predicted, the analysis adjusting for missing data (see Supplementary Materials S1.5. for details) showed increased effect sizes across the lower vmPFC where dropout was most severe (Figure 3). Activations based on SDM-Z > 2.3 uncorrected were larger in the adjusted than the original analysis for the altruistic mean activations (Figure 9a). This threshold was chosen as a common value for thresholding, close to the average of the critical SDM-Z values generated in the permutation tests for the original analyses and AES:SDM analyses run with the 50% of maps with the best coverage.

For the comparison where altruistic > strategic prosocial choices, posterior vmPFC activations were either larger than the original analysis or shown only in the adjusted analysis (Figure 9b). In the original comparison where strategic > altruistic prosocial choices, no vmPFC activation was significant when thresholded using AES:SDM permutation analysis and very little showed SDM-Z > 2.3. However, when adjusting for dropout, a small region of activation in anterior vmPFC shows SDM-Z scores greater than 2.3 (Figure 9b).
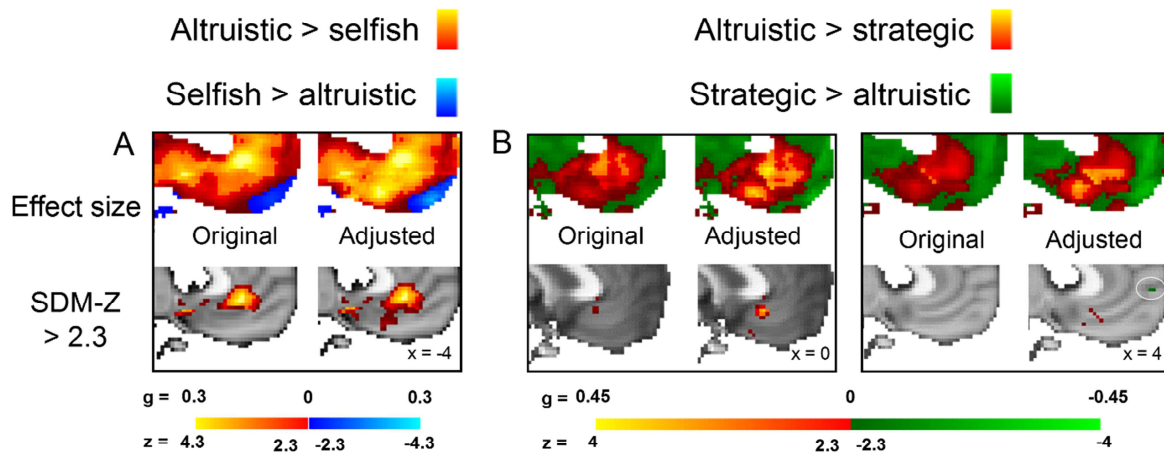
Figure 9. Adjusted analysis accounting for vmPFC dropout. Increased effect sizes (Hedges' G; top row) and larger regions showing SDM-Z > 2.3 (bottom row) in the adjusted analysis compared to the original. **A:** altruistic contrasted with selfish decisions (n = 12), **B:** comparison between altruistic and strategic decisions (n = 24). All results are from the subgroup of studies with a selfish contrast.

4. Discussion

This meta-analysis shows there is consistency in neural processes during decisions to give, using over a decade of fMRI research and over one thousand participants. Within each type of decision to give (altruistic and strategic), activations are present across a variety of tasks, suggesting common core processes. There are also differences between the two types of decisions to give, which are thought to reflect the differences in the source of reward, timing, certainty, and application of theory of mind.

We structure our discussion around the basic questions for the meta-analysis, though some discussion of contrasts inevitably crosses into more than one section. We focus on established social cognition and reward networks, given these are the most common networks discussed in the independent studies, but also highlight activations outside of this familiar territory.

All thresholded and unthresholded statistical brain maps are available at https://neurovault.org/collections/3987 and details of peaks (as well as maps) can be downloaded from https://doi.org/10.25377/sussex.c.4155923. Since a discussion of each individual activation is not feasible in this discussion, we encourage the reader to use these maps, together with provided tables, for their reference, inference, and convenience in future research.

4.1. What is common to altruistic and strategic decisions to give?

Sharing with others in either context consistently activates regions associated with reward. Compared to selfish decisions, NuAcc, vmPFC, OFC sgACC and ACC (area 32) are

more active when an individual decides to give. These regions are established elements of the reward and value-computation networks (Bartra et al., 2013). A NuAcc activation, for instance, gives a moderately strong likelihood that a reward process is occurring (Ariely and Berns, 2010) and responds to multiple reward types (Levy and Glimcher, 2012) including money, intrinsic reward (Genevsky et al., 2013; Harbaugh et al., 2007; Moll et al., 2006) and strategic cooperation (Rilling et al., 2002).

These signals may represent different concepts in the two contexts. While intrinsic reward may accompany strategic prosocial choices, these activations could also signal anticipation of an extrinsic benefit. This would suggest intrinsic altruistic motivation shares neural circuits with extrinsic motivation, supporting the common neural currency proposal (Levy and Glimcher, 2012) for multiple aspects of prosocial decision-making. Speculatively, this overlap may also explain behavioural findings of decreased altruistic behaviour, which was once freely given, following introduction of extrinsic incentives, by 'crowding out' the intrinsic motivations represented within the same neural circuits (Frey and Oberholzer-Gee, 1997). Such a conclusion however, would need direct experimentation.

Being selfish, relative to being prosocial, does not overlap much between strategic and altruistic contexts, save for a small region of the parietal operculum. This suggests the underlying processes and expectations are likely to be different. In altruistic contexts, the contrast may represent a preference for self over others or loss aversion (Tom et al., 2007). In strategic contexts, the choice is more likely driven by predictions of others' behaviour and the desire to reduce uncertainty.

As expected for any contrast with rest, altruistic and strategic generosity show overlapping widespread deactivation of the 'default mode' network and activation of the 'task-activated' network (Fox et al., 2005). These activations, such as in ACC and AI, could reflect domain-general processes such as deciding between multiple options (Kennerley et al., 2009). They could also reflect more specific processes common to both contexts, for example negative aspects of the prosocial choice including disutility (Zaki and Mitchell, 2011), distress (Zanon et al., 2014), and conflict (Koban et al., 2014). Finally, these activations could represent different processes in each context. For altruistic giving compared to rest, AI and ACC activity could underlie empathy (FeldmanHall et al., 2012; Gospic et al., 2013; Hein et al., 2010). More relevant for risky strategic giving (Apps et al., 2016), ACC activation could reflect greater ambiguity or risk (Krain et al., 2006) or an increase in effort and prediction (Vassena et al., 2017).

Regions less active than baseline during both types of decision to give include vmPFC, TPJ and STS which are implicated in both social decision-making (Decety and Lamm, 2007; Frith and Frith, 2003; Schurz et al., 2014) and resting-state networks (Damoiseaux et al., 2006; Mak et al., 2017). This fits with previous demonstrations of quantitative overlap (Acikalin et al., 2017) and discussion on what these processes may share (Mars et al., 2012). Critically, these effects highlight the importance of the control task when making inferences; the 'activation' associated with a prosocial decision might actually be *less deactivation* which only becomes evident with a comparison to rest.

4.2. What is consistent about altruistic decisions?

During altruistic decisions, the consistent activation of reward networks demonstrates that despite ending up with less extrinsic gain, the reward system is active when giving.

In addition to regions common to both types of choices to give, generous altruistic decisions compared to selfish choices activate other regions, including left dlPFC (area 8B), posterior cingulate cortex (PCC), pre-SMA and right cerebellum. In an analysis restricted to studies with a selfish choice contrast, we also found bilateral precuneus. See below for discussion of these regions.

The reverse contrast identifies additional activation for selfish choices over altruistic ones in putamen, caudate, pSTS, dlPFC (areas 46 & 9), left amygdala and, in the subgroup with selfish contrasts, bilateral posterior insula. The putamen, caudate and amygdalae have all been linked to aspects of reward processing (Haruno and Kawato, 2006; Holland and Gallagher, 2004; but see also Miller et al., 2014) and have high levels of interconnectivity (Roy et al., 2009). These parts of the reward network may be less sensitive to intrinsic rewards and more sensitive to extrinsic benefits of keeping the goods.

There have been claims the dlPFC inhibits selfish tendencies to produce prosocial decisions (Feng et al., 2015; Knoch et al., 2009, 2006; Strang et al., 2015) but also findings supporting the reverse, that the inhibition is of prosocial impulses (Christov-Moore et al., 2016; Yamagishi et al., 2016). Our finding in area 8B corresponds with the former model but our pattern of results for areas 46 and 9 fits with the latter. This anatomical differentiation could explain the differences in previous conclusions if, for example, these stimulation studies targeted different subregions. Other theories (Buckholtz, 2015; Gershman et al., 2014) suggest the lPFC could be integrating norms into decisions – disrupting right lPFC affects adherence to rules in gift-giving contexts (Gross et al., 2018).

Altogether, these results provide the signature activations of altruistic giving decisions to use in future investigations of their connectivity and more specific roles in prosocial behaviour.

4.3. What is consistent about strategic decisions?

During strategic decisions to give, reward circuit activation could represent either extrinsic reward expectancy, which is usually higher for the prosocial choice contingent on the partner's behaviour, or intrinsic satisfaction. The signature of a generous strategic decision also includes activation of precuneus, right amygdala and regions of the cerebellum. Analysis limited to studies with the selfish contrast also shows activity in right dlPFC (area 46), left amygdala and the right frontal pole.

The precuneus shows similar, but not overlapping, activation for both altruistic (bilateral) and strategic (on the left) gifts compared to their selfish alternatives. Along with the PCC being more active for altruistic than selfish decisions, these regions linked to mentalising (Cavanna and Trimble, 2006; Schurz et al., 2014; Waytz and Mitchell, 2011), empathy (Jackson et al., 2006) and guilt (Morey et al., 2012) did show results in line with increased perspective taking during prosocial choices.

Activation in the amygdala for strategic decisions fits with our interpretation of reward expectancy during selfishness in altruistic paradigms. In strategic tasks it could also be interpreted as encoding estimated immediate cost of the gift (Gospic et al., 2013). Previous studies have shown activity scales with the amount entrusted to another (Stanley et al., 2012) and is greater in real than imagined decisions (FeldmanHall et al., 2012; Gospic et al., 2013). Outside of prosocial decisions, the amygdala is associated with many other relevant processes, including loss aversion (De Martino et al., 2010), fear (Tovote et al., 2015),

aggression (Haller, 2018) and emotion processing (Janak and Tye, 2015) to name but a few. Due to the low resolution of a meta-analysis from averaging images and the broad scope of the tasks used, this study does not differentiate between specific explanations.

The consistent neural signature of keeping money in strategic contexts includes increased activity in left TPJ, anterior middle temporal regions, right temporal pole and pre and postcentral gyri. The specific analysis with selfish controls also showed activity in bilateral posterior temporal sulci, left temporal pole, left hippocampus, right supplementary motor area, right cerebellum, and right posterior insula. If TPJ and pSTS activations represent mentalising in this context, these results suggest increased processing about the second player is associated with *not* trusting, valuing, or cooperating with them. For altruistic decisions, this was also the pattern for pSTS.

These findings overall show the consistent pattern of activations during strategic giving for extrinsic rewards. Like for altruistic decisions, future work can use this to reveal the exact roles and connectivity of regions.

4.4. How do altruistic and strategic decisions (statistically) differ?

Contrasts between altruistic and strategic choices make a clear case that that these groups of tasks rely on different processes and should not be considered interchangeable in the literature.

4.4.1 Altruistic > Strategic

Altruistic choices to give correlate with greater activation in a set of reward and social cognition regions. These include sgACC, TPJ and various regions of the temporal lobes. Limiting to selfish contrasts additionally revealed right pSTS. That *any* regions show greater activity during altruistic choices challenges the idea that strategic decisions encompass all the elements of altruistic decisions.

The sgACC, which is involved in both altruistic and strategic prosocial behaviours independently, is particularly active when only intrinsic motivations are available. This region also activates during charitable donations (Moll et al., 2006), distinguishes altruism from decisions which benefit the individual (Pulcu et al., 2014) and signals prosocial learning prediction errors (Lockwood et al., 2016) as well as emotional processing in social contexts (Drevets et al., 2008). Activity in sgACC is also linked to a reduced propensity to harm others in utilitarian judgements (Wiech et al., 2013). The current meta-analytic finding adds weight to the idea that sgACC, together with a network of social cognition regions, may play a defining role in altruistic decisions to give.

4.4.2. Strategic > altruistic

Strategic decisions correlate with more activity in ventral and dorsal striatum, right dlPFC (areas 46 & 46D), right pSTS and right frontal pole. Isolating studies with a selfish contrast additionally showed posterior insula and fusiform face area activity.

Greater right NuAcc activity for strategic than altruistic choices suggests that intrinsic and extrinsic responses sum in this region, or extrinsic rewards (if supplanting intrinsic rewards) evoke stronger responses. This finding fits with behavioural findings that prosocial choices are more frequent in strategic than altruistic paradigms (Zheng and Zhu, 2013).

The left caudate also activates more for strategic than altruistic decisions, a pattern previously limited to the putamen (Weiland et al., 2012). A closer look suggests that differences in dorsal striatum between the task groups may be partly driven by greater activity for the selfish choice in altruistic contexts (a difference absent in strategic contexts). That may be due to the increase in extrinsic reward obtained by being selfish in an altruistic task whereas in strategic scenarios, selfishness often leads to a more certain but lower payment than optimum cooperation. The dorsal striatum has also been linked to habitual responses (Balleine et al., 2007; Burton et al., 2015; Everitt and Robbins, 2016) which could suggest that selfish decisions in altruistic contexts are more habitual and less goal-directed than strategic decisions to keep resources (and less sensitive to devaluation).

As expected, inferences from mentalising-associated regions are not straightforward. Compared to strategic gifts, altruistic gifts recruit more left TPJ and left anterior STS activity. Overall, when using all studies, strategic activity in right pSTS is greater than altruistic, potentially reflecting greater consideration of others' intentions. However, when limited to comparisons with a selfish choice, the altruistic choice to give shows greater activity in this region. This discrepancy may result from relatively high but *similar* levels of mentalising activity prior to either response in strategic contexts. In contrast, the differential between gifts and selfish choices is higher in altruistic contexts – gifts likely involve more other-oriented processing than selfish choices (e.g. representing the other's need or appreciation).

Outside of mentalising, previous findings show TPJ activation and connectivity also peak at maximum conflict, near the maximum one is willing to give and when temptation to be selfish is greatest (Morishima et al., 2012; Strombach et al., 2015). This conflict is likely to be highest in an altruistic context, when there is no opportunity for financial gain. Overall, these social brain regions may have different roles which are recruited to varying extents depending on the context of task and what control is used. More work is required to understand precisely what they are doing in each context.

The results for right dlPFC areas 46 and 46D are in line with findings that levels of strategic behaviour correlate with differences between ultimatum and dictator game activation and cortical thickness (on the left) in dlPFC (Steinbeis et al., 2012). Moreover, right dlPFC transcranial direct current stimulation had opposing effects on giving behaviour under altruistic and strategic conditions (Ruff et al., 2013), suggesting the exact role of the region depends on the context.

4.4.3. The vmPFC

Analysis across a ROI axis in the vmPFC, particularly when adjusted for signal dropout, suggests altruistic activation *declines* moving anteriorly in the brain as strategic activation *increases*. Along the same axis, regions of vmPFC show differing connectivity patterns (Gallardo et al., 2017): posterior areas connect locally and to limbic regions while anterior areas are grouped with distant mentalising regions (Alcalá-López et al., 2017). Anterior areas are also directly involved in mentalising under conditions of ambiguity, a key feature of strategic tasks (Jenkins and Mitchell, 2010). A similar axis identifies the influence of certain social inferences on value judgements (Campbell-Meiklejohn et al., 2016; De Martino et al., 2017). Contrasts of this meta-analysis reflect within-participant comparisons. Looking between participants, selfish and prosocial individuals also differentially activate a similar vmPFC axis during consideration of benefits to the self and benefits to others (Sul et al., 2015).

With relevance to the nature of intrinsic reward, previous meta-analyses have suggested concrete primary (food or erotic) and abstract secondary (monetary) rewards are represented more posterior and anterior respectively (Clithero and Rangel, 2013; Sescousse et al., 2013). By this, increased strategic activation further forward in vmPFC could be interpreted as a reflection of secondary (primarily monetary) rewards, whereas altruistic warm glow may activate areas similar to primary rewards.

There are also other differences between altruistic and strategic decisions, such as the certainty and timing of available rewards that may underlie differences this trajectory, requiring further study to rule these in or out as explanations.

4.5. Methodological contributions

We developed a novel method to adjust for dropout when combining effect sizes in a random-effects model that may be useful in future meta-analyses. Results suggests the role of vmPFC in prosocial decision-making may be underestimated due to a lack of coverage in the region. Future fMRI studies on this topic should always utilise methods to minimise this problem (Domsch et al., 2013; Fernandez et al., 2017; Weiskopf et al., 2007) and report the coverage of the region if focusing on the vmPFC.

This study also highlights the importance of a comparison to a selfish control for interpretation of findings. Generous and selfish choices in strategic tasks similarly involve mentalising and extrinsic rewards, making them more similar than altruistic gifts and their selfish alternatives. The latter put extrinsic and intrinsic motivations in direct competition. This point may explain discrepancies between the two previous studies comparing altruistic dictator and strategic ultimatum games (Weiland et al., 2012; Zheng and Zhu, 2013).

4.6. Limitations

Applying fMRI meta-analysis to prosocial decisions identifies consistent activations across studies, tasks and controls. However, averaging ignores connectivity (Hein et al., 2016) and individual differences such as social value orientation (Emonds et al., 2014, 2011; Fermin et al., 2016), attachment style (Schneider-Hassloff et al., 2015), age (Fett et al., 2014), gender (Krach et al., 2009) and personality (Garbarini et al., 2014). This paper includes the decisions of 1150 participants but there are more published studies than had maps or coordinates available for analysis.

Even if all published papers on prosocial decisions had been included, conclusions would be limited to specific experimental settings. The separation between altruistic and strategic decisions which arises from tightly controlled games is only an abstraction of real-world decisions. The real world provides opportunities for strategic and altruistic motivations to work together (e.g. picking the ideal present, effective altruism and others) that neuroimaging studies are now only beginning to explore. Moreover the lab differs from the real world in other respects. For instance, is difficult to measure reputational motivation in lab-based altruistic studies. There is no way to completely prevent the participant considering the experimenter's view of them or their decisions so reputational concerns may differ from real-world donation contexts.

The selfish choice was the most common control condition used in the data we received. However, some research suggests that the contrast of prosocial with selfish choices can be complicated to interpret and can be influenced by context (Krajbich et al.,

2015). The vmPFC region identified in this meta-analysis has been linked to the overall value of a prosocial decision and therefore how long it takes to make (Hutcherson et al., 2015). It was not possible to incorporate response time into the present analysis, due to under reporting of reaction times and reliance on group averages.

This meta-analysis also grouped different paradigms together under themes (i.e. multiple economic games). To precisely control for and differentiate the effects unique to individual paradigms would require tightly controlled individual studies or many times the number of available studies.

5. Conclusion

This study is the first systematic fMRI meta-analysis to demonstrate the consistency and differentiation of neural correlates for strategic and altruistic prosocial decisions. We identify the locations of reliable activations for two different types of prosocial choice.

While we knew both types of gift benefit others, we show that both are also consistently rewarding to the giver and share many neural substrates. In contrast, mechanisms for the decision not to give appears to vary, depending on the strategic context.

Despite some similarities, altruistic and strategic decisions to give are not interchangeable in the brain. The potential for an extrinsic benefit changes the neural mechanism at the point of choice in both level and location of activation. Of the regions involved in prosocial choices overall, sgACC activated more for altruistic than strategic decisions and NuAcc was more active for strategic than altruistic choices. That any region is more involved in altruistic decisions suggests that there is something additive and special about giving when the only benefit is a warm glow. Greater reward-network activity for strategic decisions is in line with and may account for higher rates of prosocial choices in these contexts, compared to altruistic ones.

Across regions linked to social cognition, results were mixed, reflecting the complexity and diversity of theory of mind application in our social lives.

The changing cytoarchitecture across the vmPFC also differentiates strategic and altruistic gifts. Activity increased for strategic and decreased for altruistic choices along a posterior to anterior axis in a way that relates well to what we know about the connectivity and functions across this region.

Methodologically, we provide an additional step forward in the methods of meta-analyses to account for variable signal dropout between fMRI studies.

With consistent effects in hand, the field can move forward with focused examination to distinguish between competing interpretations of each region's role in prosocial decision-making.

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References

Acikalin, M.Y., Gorgolewski, K.J., Poldrack, R.A., 2017. A coordinate-based meta-analysis of overlaps in regional specialization and functional connectivity across subjective value and default mode networks. Front. Neurosci. 11, 1. https://doi.org/10.3389/fnins.2017.00001

Alcalá-López, D., Smallwood, J., Jefferies, E., Van Overwalle, F., Vogeley, K., Mars, R.B., Turetsky, B.I., Laird, A.R., Fox, P.T., Eickhoff, S.B., Bzdok, D., 2017. Computing the social brain connectome across systems and states. Cereb. Cortex 1–26. https://doi.org/10.1093/cercor/bhx121

Andreoni, J., 1990. Impure altruism and donations to public goods: A theory of warm-glow giving. Econ. J. 100, 464–477.

Andreoni, J., 1989. Giving with impure altruism: Applications to charity and ricardian equivalence. J. Polit. Econ. 97, 1447. https://doi.org/10.1086/261662

Apps, M.A.J., Rushworth, M.F.S., Chang, S.W.C., 2016. The anterior cingulate gyrus and social cognition: Tracking the motivation of others. Neuron. https://doi.org/10.1016/j.neuron.2016.04.018

Ariely, D., Berns, G.S., 2010. Neuromarketing: the hope and hype of neuroimaging in business. Nat. Rev. Neurosci. 11, 284–292. https://doi.org/10.1038/nrn2795

Balleine, B.W., Delgado, M.R., Hikosaka, O., 2007. The role of the dorsal striatum in reward and decision-making. J. Neurosci. 27, 8161–8165. https://doi.org/10.1523/JNEUROSCI.1554-07.2007

Bartra, O., McGuire, J.T., Kable, J.W., 2013. The valuation system: A coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value. Neuroimage 76, 412–427. https://doi.org/10.1016/j.neuroimage.2013.02.063

Bellucci, G., Chernyak, S. V., Goodyear, K., Eickhoff, S.B., Krueger, F., 2017. Neural signatures of trust in reciprocity: A coordinate-based meta-analysis. Hum. Brain Mapp. 38, 1233–1248. https://doi.org/10.1002/hbm.23451

Berg, J., Dickhaut, J., McCabe, K., 1995. Trust, reciprocity, and social history. Games Econ. Behav. 10, 122–142. https://doi.org/10.1006/game.1995.1027

Buckholtz, J.W., 2015. Social norms, self-control, and the value of antisocial behavior. Curr. Opin. Behav. Sci. 3, 122–129. https://doi.org/10.1016/J.COBEHA.2015.03.004

Burton, A.C., Nakamura, K., Roesch, M.R., 2015. From ventral-medial to dorsal-lateral striatum: Neural correlates of reward-guided decision-making. Neurobiol. Learn. Mem. https://doi.org/10.1016/j.nlm.2014.05.003

Button, K.S., Ioannidis, J.P. a, Mokrysz, C., Nosek, B. a, Flint, J., Robinson, E.S.J., Munafò, M.R., 2013. Power failure: Why small sample size undermines the reliability of neuroscience. Nat. Rev. Neurosci. 14, 365–76. https://doi.org/10.1038/nrn3475

Campbell-Meiklejohn, D., Simonsen, A., Frith, C.D., Daw, N.D., 2016. Independent neural computation of value from the confidence of others. J. Neurosci. 37, 4490–15. https://doi.org/10.1523/JNEUROSCI.4490-15.2016

Capraro, V., 2017. Do the right thing: Preferences for moral behavior, rather than equity or efficiency per se, drive human prosociality. SSRN Electron. J. 13, 99–111. https://doi.org/10.2139/ssrn.2965067

Cavanna, A.E., Trimble, M.R., 2006. The precuneus: A review of its functional anatomy and

behavioural correlates. Brain 129, 564–583. https://doi.org/10.1093/brain/awl004

Chaudhuri, A., 2011. Sustaining cooperation in laboratory public goods experiments: A selective survey of the literature. Exp. Econ. 14, 47–83. https://doi.org/10.1007/s10683-010-9257-1

Christov-Moore, L., Sugiyama, T., Grigaityte, K., Iacoboni, M., 2016. Increasing generosity by disrupting prefrontal cortex. Soc. Neurosci. 1–8. https://doi.org/10.1080/17470919.2016.1154105

Clithero, J.A., Rangel, A., 2013. Informatic parcellation of the network involved in the computation of subjective value. Soc. Cogn. Affect. Neurosci. 9, 1289–1302. https://doi.org/10.1093/scan/nst106

Cremers, H.R., Wager, T.D., Yarkoni, T., 2017. The relation between statistical power and inference in fMRI. PLoS One 12, e0184923. https://doi.org/10.1371/journal.pone.0184923

Damoiseaux, J.S., Rombouts, S.A.R.B., Barkhof, F., Scheltens, P., Stam, C.J., Smith, S.M., Beckmann, C.F., 2006. Consistent resting-state networks across healthy subjects. Proc. Natl. Acad. Sci. 103, 13848–13853. https://doi.org/10.1073/pnas.0601417103

De Martino, B., Bobadilla-Suarez, S., Nouguchi, T., Sharot, T., Love, B.C., 2017. Social information is integrated into value and confidence judgments according to its reliability. J. Neurosci. 37, 6066–6074. https://doi.org/10.1523/JNEUROSCI.3880-16.2017

De Martino, B., Camerer, C.F., Adolphs, R., 2010. Amygdala damage eliminates monetary loss aversion. Proc. Natl. Acad. Sci. 107, 3788–3792. https://doi.org/10.1073/pnas.0910230107

Decety, J., Bartal, I.B., Uzefovsky, F., Knafo-noam, A., 2015. Empathy as a driver of prosocial behaviour: Highly conserved neurobehavioural mechanisms across species. Philos. Trans. R. Soc. B, Biol. Sci. 371, 20150077. https://doi.org/http://dx.doi.org/10.1098/rstb.2015.0077

Decety, J., Lamm, C., 2007. The role of the right temporoparietal junction in social interaction: How low-level computational processes contribute to meta-cognition. Neurosci. 13, 580–93. https://doi.org/10.1177/1073858407304654

Domsch, S., Linke, J., Heiler, P.M., Kroll, A., Flor, H., Wessa, M., Schad, L.R., 2013. Increased BOLD sensitivity in the orbitofrontal cortex using slice-dependent echo times at 3 T. Magn. Reson. Imaging 31, 201–211. https://doi.org/10.1016/j.mri.2012.06.020

Drevets, W.C., Savitz, J., Trimble, M., 2008. The subgenual anterior cingulate cortex in mood disorders. CNS Spectr. 13, 663–681. https://doi.org/10.1017/S1092852900013754

Eklund, A., Nichols, T.E., Knutsson, H., 2016. Cluster failure: Why fMRI inferences for spatial extent have inflated false-positive rates. Proc. Natl. Acad. Sci. U. S. A. 113, 7900–5. https://doi.org/10.1073/pnas.1602413113

Emonds, G., Declerck, C.H., Boone, C., Seurinck, R., Achten, R., 2014. Establishing cooperation in a mixed-motive social dilemma. An fMRI study investigating the role of social value orientation and dispositional trust. Soc. Neurosci. 9, 10–22. https://doi.org/10.1080/17470919.2013.858080

Emonds, G., Declerck, C.H., Boone, C., Vandervliet, E.J.M., Parizel, P.M., 2011. Comparing the neural basis of decision making in social dilemmas of people with different social value orientations, an fMRI study. J. Neurosci. Psychol. Econ. 4, 11–24. https://doi.org/10.1037/a0020151

Everitt, B.J., Robbins, T.W., 2016. Drug addiction: Updating actions to habits to compulsions ten years on. Annu. Rev. Psychol. 67, 23–50. https://doi.org/10.1146/annurev-psych-122414-033457

Falk, A., Fischbacher, U., 2006. A theory of reciprocity. Games Econ. Behav. 54, 293–315. https://doi.org/10.1016/j.geb.2005.03.001

Fehr, E., Fischbacher, U., 2004. Social norms and human cooperation. Trends Cogn. Sci. 8, 185–190. https://doi.org/10.1016/j.tics.2004.02.007

Fehr, E., Fischbacher, U., Gächter, S., 2002. Strong reciprocity, human cooperation, and the enforcement of social norms. Hum. Nat. 13, 1–25. https://doi.org/10.1007/s12110-002-1012-7

Fehr, E., Gächter, S., 2002. Altruistic punishment in humans. Nature 415, 137–140. https://doi.org/10.1038/415137a

FeldmanHall, O., Dalgleish, T., Evans, D., Mobbs, D., 2015. Empathic concern drives costly altruism. Neuroimage 105, 347–356. https://doi.org/10.1016/j.neuroimage.2014.10.043

FeldmanHall, O., Dalgleish, T., Thompson, R., Evans, D., Schweizer, S., Mobbs, D., 2012. Differential neural circuitry and self-interest in real vs hypothetical moral decisions. Soc. Cogn. Affect. Neurosci. 7, 743–751. https://doi.org/10.1093/scan/nss069

Feng, C., Luo, Y.J., Krueger, F., 2015. Neural signatures of fairness-related normative decision making in the ultimatum game: A coordinate-based meta-analysis. Hum. Brain Mapp. 36, 591–602. https://doi.org/10.1002/hbm.22649

Fermin, A.S.R., Sakagami, M., Kiyonari, T., Li, Y., Matsumoto, Y., Yamagishi, T., 2016. Representation of economic preferences in the structure and function of the amygdala and prefrontal cortex. Sci. Rep. 6, 20982. https://doi.org/10.1038/srep20982

Fernandez, B., Leuchs, L., Sämann, P.G., Czisch, M., Spoormaker, V.I., 2017. Multi-echo EPI of human fear conditioning reveals improved BOLD detection in ventromedial prefrontal cortex. Neuroimage 156, 65–77. https://doi.org/10.1016/j.neuroimage.2017.05.005

Fett, A.K.J., Gromann, P.M., Giampietro, V., Shergill, S.S., Krabbendam, L., 2014. Default distrust? An fMRI investigation of the neural development of trust and cooperation. Soc. Cogn. Affect. Neurosci. 9, 395–402. https://doi.org/10.1093/scan/nss144

Filkowski, M., Cochran, R.N., Haas, B., 2016. Altruistic behavior: mapping responses in the brain. Neurosci. Neuroeconomics 5, 65–75. https://doi.org/10.2147/NAN.S87718

Fox, M.D., Snyder, A.Z., Vincent, J.L., Corbetta, M., Van Essen, D.C., Raichle, M.E., 2005. The human brain is intrinsically organized into dynamic, anticorrelated functional networks. Proc. Natl. Acad. Sci. 102, 9673–9678. https://doi.org/10.1073/pnas.0504136102

Frey, B.S., Oberholzer-Gee, F., 1997. The cost of price incentives: An empirical analysis of motivation crowding-out. Am. Econ. Rev. 87, 746–755. https://doi.org/10.1207/2951373

Frith, C.D., Frith, U., 2006. The neural basis of mentalizing. Neuron 50. https://doi.org/10.1016/j.neuron.2006.05.001

Frith, U., Frith, C.D., 2003. Development and neurophysiology of mentalizing. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 358, 459–73. https://doi.org/10.1098/rstb.2002.1218

Gabay, A.S., Radua, J., Kempton, M.J., Mehta, M.A., 2014. The Ultimatum Game and the brain: A meta-analysis of neuroimaging studies. Neurosci. Biobehav. Rev. 47, 549–558. https://doi.org/10.1016/j.neubiorev.2014.10.014

Gallardo, G., Fick, R., Wells, W., Deriche, R., Wassermann, D., 2017. Groupwise structural parcellation of the cortex: A sound approach based on logistic models, in: Mathematics and Visualization. pp. 99–112. https://doi.org/10.1007/978-3-319-54130-3_8

Garbarini, F., Boero, R., D'Agata, F., Bravo, G., Mosso, C., Cauda, F., Duca, S., Geminiani, G., Sacco, K., 2014. Neural correlates of gender differences in reputation building. PLoS One 9. https://doi.org/10.1371/journal.pone.0106285

Genevsky, A., Västfjäll, D., Slovic, P., Knutson, B., 2013. Neural underpinnings of the identifiable victim effect: Affect shifts preferences for giving. J. Neurosci. 33, 17188–17196. https://doi.org/10.1523/JNEUROSCI.2348-13.2013

Gershman, S.J., Markman, A.B., Otto, A.R., 2014. Retrospective revaluation in sequential decision making: A tale of two systems. J. Exp. Psychol. Gen. 143, 182–194. https://doi.org/10.1037/a0030844

Gospic, K., Sundberg, M., Maeder, J., Fransson, P., Petrovic, P., Isacsson, G., Karlström, A., Ingvar, M., 2013. Altruism costs-the cheap signal from amygdala. Soc. Cogn. Affect. Neurosci. 9, 1325–1332. https://doi.org/10.1093/scan/nst118

Gross, J., Emmerling, F., Vostroknutov, A., Sack, A.T., 2018. Manipulation of pro-sociality and rule-following with non-invasive brain stimulation. Sci. Rep. 8, 1827. https://doi.org/10.1038/s41598-018-19997-5

Güth, W., Schmittberger, R., Schwarze, B., 1982. An experimental analysis of ultimatum bargaining. J. Econ. Behav. Organ. 3, 367–388. https://doi.org/10.1016/0167-2681(82)90011-7

Haller, J., 2018. The role of central and medial amygdala in normal and abnormal aggression: A review of classical approaches. Neurosci. Biobehav. Rev. https://doi.org/10.1016/j.neubiorev.2017.09.017

Harbaugh, W.T., Mayr, U., Burghart, D.R., 2007. Neural responses to taxation and voluntary giving reveal motives for charitable donations. Science (80-.). 316, 1622–1625. https://doi.org/10.1126/science.1140738

Hare, T.A., Camerer, C.F., Knoepfle, D.T., O'Doherty, J.P., Rangel, A., 2010. Value computations in ventral medial prefrontal cortex during charitable decision making incorporate input from regions involved in social cognition. J. Neurosci. 30, 583–590. https://doi.org/10.1523/JNEUROSCI.4089-09.2010

Haruno, M., Kawato, M., 2006. Different neural correlates of reward expectation and reward expectation error in the putamen and caudate nucleus during stimulus-action-reward association learning. J. Neurophysiol. 95, 948–959. https://doi.org/10.1152/jn.00382.2005

Hein, G., Morishima, Y., Leiberg, S., Sul, S., Fehr, E., 2016. The brains functional network architecture reveals human motives. Science (80-.). 351, 1074–1078. https://doi.org/10.1126/science.aac7992

Hein, G., Silani, G., Preuschoff, K., Batson, C.D., Singer, T., 2010. Neural responses to ingroup and outgroup members' suffering predict individual differences in costly helping. Neuron 68, 149–160. https://doi.org/10.1016/j.neuron.2010.09.003

Holland, P.C., Gallagher, M., 2004. Amygdala-frontal interactions and reward expectancy. Curr. Opin. Neurobiol. https://doi.org/10.1016/j.conb.2004.03.007

Hutcherson, C.A., Bushong, B., Rangel, A., 2015. A neurocomputational model of altruistic choice and its implications. Neuron 87, 451–462. https://doi.org/10.1016/j.neuron.2015.06.031

Izuma, K., Saito, D.N., Sadato, N., 2010. Processing of the incentive for social approval in the ventral striatum during charitable donation. J. Cogn. Neurosci. 22, 621–631. https://doi.org/10.1162/jocn.2009.21228

Jackson, P.L., Brunet, E., Meltzoff, A.N., Decety, J., 2006. Empathy examined through the neural mechanisms involved in imagining how I feel versus how you feel pain. Neuropsychologia 44, 752–761. https://doi.org/10.1016/j.neuropsychologia.2005.07.015

Janak, P.H., Tye, K.M., 2015. From circuits to behaviour in the amygdala. Nature. https://doi.org/10.1038/nature14188

Jenkins, A.C., Mitchell, J.P., 2010. Mentalizing under uncertainty: Dissociated neural responses to ambiguous and unambiguous mental state inferences. Cereb. Cortex 20, 404–410. https://doi.org/10.1093/cercor/bhp109

Kahneman, D., Knetsch, J.L., Thaler, R.H., 1986. Fairness and the assumptions of economics. J. Bus. 59, S285. https://doi.org/10.1086/296367

Kennerley, S.W., Dahmubed, A.F., Lara, A.H., Wallis, J.D., 2009. Neurons in the frontal lobe encode the value of multiple decision variables. J. Cogn. Neurosci. 21, 1162–78. https://doi.org/10.1162/jocn.2009.21100

Knoch, D., Gianotti, L.R.R., Pascual-Leone, A., Treyer, V., Regard, M., Hohmann, M., Brugger, P., 2006. Disruption of right prefrontal cortex by low-frequency repetitive transcranial magnetic stimulation induces risk-taking behavior. J. Neurosci. 26, 6469–6472. https://doi.org/10.1523/jneurosci.0804-06.2006

Knoch, D., Schneider, F., Schunk, D., Hohmann, M., Fehr, E., 2009. Disrupting the prefrontal cortex diminishes the human ability to build a good reputation. Proc. Natl. Acad. Sci. U. S. A. 106, 20895–9. https://doi.org/10.1073/pnas.0911619106

Koban, L., Pichon, S., Vuilleumier, P., 2014. Responses of medial and ventrolateral prefrontal cortex to interpersonal conflict for resources. Soc. Cogn. Affect. Neurosci. 9, 561–569. https://doi.org/10.1093/scan/nst020

Krach, S., Blümel, I., Marjoram, D., Lataster, T., Krabbendam, L., Weber, J., van Os, J., Kircher, T., 2009. Are women better mindreaders? Sex differences in neural correlates of mentalizing detected with functional MRI. BMC Neurosci. 10. https://doi.org/10.1186/1471-2202-10-9

Krain, A.L., Wilson, A.M., Arbuckle, R., Castellanos, F.X., Milhama, M.P., 2006. Distinct neural mechanisms of risk and ambiguity: A meta-analysis of decision-making. Neuroimage 32, 477–484. https://doi.org/10.1016/j.neuroimage.2006.02.047

Krajbich, I., Bartling, B., Hare, T., Fehr, E., 2015. Rethinking fast and slow based on a critique of reaction-time reverse inference. Nat. Commun. 6, 7455. https://doi.org/10.1038/ncomms8455

Levy, D.J., Glimcher, P.W., 2012. The root of all value: A neural common currency for choice. Curr. Opin. Neurobiol. 22, 1027–1038. https://doi.org/10.1016/j.conb.2012.06.001

Lockwood, P.L., Apps, M.A.J., Roiser, J.P., Viding, E., 2015. Encoding of vicarious reward prediction in anterior cingulate cortex and relationship with trait empathy. J. Neurosci. 35, 13720–7. https://doi.org/10.1523/JNEUROSCI.1703-15.2015

Lockwood, P.L., Apps, M.A.J., Valton, V., Viding, E., Roiser, J.P., 2016. Neurocomputational mechanisms of prosocial learning and links to empathy. Proc. Natl. Acad. Sci. 113, 9763–9768. https://doi.org/10.1073/pnas.1603198113

Luce, R.D., Raiffa, H., 1957. Games and decisions: Introduction and critical survey., Games and decisions: Introduction and critical survey. Wiley, Oxford, England.

Luo, J., 2018. The neural basis of and a common neural circuitry in different types of pro-social behavior. Front. Psychol. 9, 859. https://doi.org/10.3389/fpsyg.2018.00859

Mackey, S., Petrides, M., 2010. Quantitative demonstration of comparable architectonic areas within the ventromedial and lateral orbital frontal cortex in the human and the macaque monkey brains. Eur. J. Neurosci. 32, 1940–1950. https://doi.org/10.1111/j.1460-9568.2010.07465.x

Mak, L.E., Minuzzi, L., MacQueen, G., Hall, G., Kennedy, S.H., Milev, R., 2017. The default mode eetwork in healthy individuals: A systematic review and meta-analysis. Brain Connect. 7, 25–33. https://doi.org/10.1089/brain.2016.0438

Mars, R.B., Neubert, F.-X., Noonan, M.P., Sallet, J., Toni, I., Rushworth, M.F.S., 2012. On the relationship between the "default mode network" and the "social brain." Front. Hum. Neurosci. 6, 1–9. https://doi.org/10.3389/fnhum.2012.00189

Milinski, M., Semmann, D., Bakker, T.C.M., Krambeck, H.J., 2001. Cooperation through indirect reciprocity: Image scoring or standing strategy? Proc. R. Soc. B Biol. Sci. 268, 2495–2501. https://doi.org/10.1098/rspb.2001.1809

Miller, E.M., Shankar, M.U., Knutson, B., McClure, S.M., 2014. Dissociating motivation from reward in human striatal activity. J. Cogn. Neurosci. 26, 1075–1084. https://doi.org/10.1162/jocn_a_00535

Mobbs, D., Yu, R., Meyer, M., Passamonti, L., Seymour, B., Calder, A.J., Schweizer, S., Frith, C.D., Dalgleish, T., 2009. A key role for similarity in vicarious reward. Science (80-.). 324, 900. https://doi.org/10.1126/science.1170539

Moher, D., Liberati, A., Tetzlaff, J., Altman, D.G., PRISMA Group, 2009. Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. BMJ 339, b2535. https://doi.org/10.1136/bmj.b2535

Moll, J., Krueger, F., Zahn, R., Pardini, M., de Oliveira-Souza, R., Grafman, J., 2006. Human fronto-mesolimbic networks guide decisions about charitable donation. Proc. Natl. Acad. Sci. U. S. A. 103, 15623–15628. https://doi.org/10.1073/pnas.0604475103

Morey, R.A., McCarthy, G., Selgrade, E.S., Seth, S., Nasser, J.D., LaBar, K.S., 2012. Neural systems for guilt from actions affecting self versus others. Neuroimage 60, 683–692. https://doi.org/10.1016/j.neuroimage.2011.12.069

Morishima, Y., Schunk, D., Bruhin, A., Ruff, C.C., Fehr, E., 2012. Linking brain structure and activation in temporoparietal junction to explain the neurobiology of human altruism. Neuron 75, 73–79. https://doi.org/10.1016/j.neuron.2012.05.021

Müller, V.I., Cieslik, E.C., Laird, A.R., Fox, P.T., Radua, J., Mataix-Cols, D., Tench, C.R., Yarkoni, T., Nichols, T.E., Turkeltaub, P.E., Wager, T.D., Eickhoff, S.B., 2018. Ten simple rules for neuroimaging meta-analysis. Neurosci. Biobehav. Rev. https://doi.org/10.1016/j.neubiorev.2017.11.012

Neubert, F.-X., Mars, R.B., Sallet, J., Rushworth, M.F.S., 2015. Connectivity reveals relationship of brain areas for reward-guided learning and decision making in human and monkey frontal cortex. Proc. Natl. Acad. Sci. 112, E2695–E2704. https://doi.org/10.1073/pnas.1410767112

Nicolle, A., Klein-Flügge, M.C., Hunt, L.T., Vlaev, I., Dolan, R.J., Behrens, T.E.J.J., 2012. An agent independent axis for executed and modeled choice in medial prefrontal cortex. Neuron 75, 1114–1121. https://doi.org/10.1016/j.neuron.2012.07.023

Niemi, L., Wasserman, E., Young, L., 2017. The behavioral and neural signatures of distinct conceptions of fairness. Soc. Neurosci. 00, 1–17. https://doi.org/10.1080/17470919.2017.1333452

Nowak, M. a, Sigmund, K., 2005. Evolution of indirect reciprocity. Nature 437, 1291–1298. https://doi.org/10.1038/nature04131

Ojemann, J.G., Akbudak, E., Snyder, A.Z., McKinstry, R.C., Raichle, M.E., Conturo, T.E., 1997. Anatomic localization and quantitative analysis of gradient refocused echo-planar fMRI susceptibility artifacts. Neuroimage 6, 156–167. https://doi.org/10.1006/nimg.1997.0289

Pulcu, E., Zahn, R., Moll, J., Trotter, P.D., Thomas, E.J., Juhasz, G., Deakin, J.F.W., Anderson, I.M., Sahakian, B.J., Elliott, R., 2014. Enhanced subgenual cingulate response to altruistic decisions in remitted major depressive disorder. NeuroImage Clin. 4, 701–710. https://doi.org/10.1016/j.nicl.2014.04.010

Radua, J., Mataix-Cols, D., 2012. Meta-analytic methods for neuroimaging data explained. Biol. Mood Anxiety Disord. 2, 6. https://doi.org/10.1186/2045-5380-2-6

Radua, J., Mataix-Cols, D., Phillips, M.L., El-Hage, W., Kronhaus, D.M., Cardoner, N., Surguladze, S., 2012. A new meta-analytic method for neuroimaging studies that combines reported peak coordinates and statistical parametric maps. Eur. Psychiatry 27, 605–611. https://doi.org/10.1016/j.eurpsy.2011.04.001

Radua, J., Rubia, K., Canales-Rodríguez, E.J., Pomarol-Clotet, E., Fusar-Poli, P., Mataix-Cols, D., 2014. Anisotropic kernels for coordinate-based meta-analyses of neuroimaging studies. Front. Psychiatry 5, 1–8. https://doi.org/10.3389/fpsyt.2014.00013

Rapoport, A., 1987. Research paradigms and expected utility models for the provision of step-level public goods. Psychol. Rev. 94, 74–83. https://doi.org/10.1037/0033-295X.94.1.74

Rilling, J.K., Gutman, D.A., Zeh, T.R., Pagnoni, G., Berns, G.S., Kilts, C.D., 2002. A neural basis for social cooperation. Neuron 35, 395–405. https://doi.org/10.1016/S0896-6273(02)00755-9

Roy, A.K., Shehzad, Z., Margulies, D.S., Kelly, A.M.C., Uddin, L.Q., Gotimer, K., Biswal, B.B., Castellanos, F.X., Milham, M.P., 2009. Functional connectivity of the human amygdala using resting state fMRI. Neuroimage 45, 614–626. https://doi.org/10.1016/j.neuroimage.2008.11.030

Ruff, C.C., Ugazio, G., Fehr, E., 2013. Changing social norm compliance with noninvasive brain stimulation. Science (80-.). 342, 482–484. https://doi.org/10.1126/science.1241399

Sallet, J., Mars, R.B., Noonan, M.P., Neubert, F.-X., Jbabdi, S., O'Reilly, J.X., Filippini, N., Thomas, A.G., Rushworth, M.F., 2013. The organization of dorsal frontal cortex in humans and macaques. J. Neurosci. 33, 12255–12274. https://doi.org/10.1523/JNEUROSCI.5108-12.2013

Schneider-Hassloff, H., Straube, B., Nuscheler, B., Wemken, G., Kircher, T., 2015. Adult attachment style modulates neural responses in a mentalizing task. Neuroscience 303, 462–473. https://doi.org/10.1016/j.neuroscience.2015.06.062

Schurz, M., Radua, J., Aichhorn, M., Richlan, F., Perner, J., 2014. Fractionating theory of mind: A meta-analysis of functional brain imaging studies. Neurosci. Biobehav. Rev. 42, 9–34. https://doi.org/10.1016/j.neubiorev.2014.01.009

Sepulcre, J., Liu, H., Talukdar, T., Martincorena, I., Thomas Yeo, B.T., Buckner, R.L., 2010. The organization of local and distant functional connectivity in the human brain. PLoS Comput. Biol. 6, 1–15. https://doi.org/10.1371/journal.pcbi.1000808

Sescousse, G., Caldú, X., Segura, B., Dreher, J.C., 2013. Processing of primary and secondary rewards: A quantitative meta-analysis and review of human functional neuroimaging studies. Neurosci. Biobehav. Rev. 37, 681–696. https://doi.org/10.1016/j.neubiorev.2013.02.002

Stanley, D.A., Sokol-Hessner, P., Fareri, D.S., Perino, M.T., Delgado, M.R., Banaji, M.R., Phelps, E.A., 2012. Race and reputation: Perceived racial group trustworthiness influences the neural correlates of trust decisions. Philos. Trans. R. Soc. B Biol. Sci. 367, 744–753. https://doi.org/10.1098/rstb.2011.0300

Steinbeis, N., Bernhardt, B.C., Singer, T., 2012. Impulse control and underlying functions of the left DLPFC mediate age-related and age-independent individual differences in strategic social behavior. Neuron 73, 1040–1051. https://doi.org/10.1016/j.neuron.2011.12.027

Strang, S., Gross, J., Schuhmann, T., Riedl, A., Weber, B., Sack, A.T., 2015. Be nice if you have to — the neurobiological roots of strategic fairness. Soc. Cogn. Affect. Neurosci. 10, 790–796. https://doi.org/10.1093/scan/nsu114

Strombach, T., Weber, B., Hangebrauk, Z., Kenning, P., Karipidis, I.I., Tobler, P.N., Kalenscher, T., 2015. Social discounting involves modulation of neural value signals by temporoparietal junction. Proc. Natl. Acad. Sci. USA 112, 1619–1624. https://doi.org/10.1073/pnas.1414715112

Sul, S., Tobler, P.N., Hein, G., Leiberg, S., Jung, D., Fehr, E., Kim, H., 2015. Spatial gradient in value representation along the medial prefrontal cortex reflects individual differences in prosociality. Proc. Natl. Acad. Sci. 112, 201423895. https://doi.org/10.1073/pnas.1423895112

Telzer, E.H., Masten, C.L., Berkman, E.T., Lieberman, M.D., Fuligni, A.J., 2011. Neural regions associated with self control and mentalizing are recruited during prosocial behaviors towards the family. Neuroimage 58, 242–249. https://doi.org/10.1016/j.neuroimage.2011.06.013

Tom, S.M., Fox, C.R., Trepel, C., Poldrack, R.A., 2007. The neural basis of loss aversion in decision-making under risk. Science (80-.). 315, 515–518. https://doi.org/10.1126/science.1134239

Tovote, P., Fadok, J.P., Lüthi, A., 2015. Neuronal circuits for fear and anxiety. Nat. Rev. Neurosci. https://doi.org/10.1038/nrn3945

Tusche, A., Bockler, A., Kanske, P., Trautwein, F.-M., Singer, T., 2016. Decoding the charitable brain: Empathy, perspective taking, and attention shifts differentially predict altruistic giving. J. Neurosci. 36, 4719–4732. https://doi.org/10.1523/JNEUROSCI.3392-15.2016

Vassena, E., Holroyd, C.B., Alexander, W.H., 2017. Computational models of anterior cingulate cortex: At the crossroads between prediction and effort. Front. Neurosci. 11, 316. https://doi.org/10.3389/fnins.2017.00316

Wager, T.D., Lindquist, M., Kaplan, L., 2007. Meta-analysis of functional neuroimaging data: Current and future directions. Soc. Cogn. Affect. Neurosci. 2, 150–158. https://doi.org/10.1093/scan/nsm015

Wager, T.D., Lindquist, M.A., Nichols, T.E., Kober, H., Van Snellenberg, J.X., 2009.

Evaluating the consistency and specificity of neuroimaging data using meta-analysis. Neuroimage. https://doi.org/10.1016/j.neuroimage.2008.10.061

Waytz, A., Mitchell, J.P., 2011. Two mechanisms for simulating other minds: Dissociations between mirroring and self-projection. Curr. Dir. Psychol. Sci. 20, 197–200. https://doi.org/10.1177/0963721411409007

Weiland, S., Hewig, J., Hecht, H., Mussel, P., Miltner, W.H.R., 2012. Neural correlates of fair behavior in interpersonal bargaining. Soc. Neurosci. 7, 537–551. https://doi.org/10.1080/17470919.2012.674056

Weiskopf, N., Hutton, C., Josephs, O., Turner, R., Deichmann, R., 2007. Optimized EPI for fMRI studies of the orbitofrontal cortex: Compensation of susceptibility-induced gradients in the readout direction. Magn. Reson. Mater. Physics, Biol. Med. 20, 39–49. https://doi.org/10.1007/s10334-006-0067-6

Wiech, K., Kahane, G., Shackel, N., Farias, M., Savulescu, J., Tracey, I., 2013. Cold or calculating? Reduced activity in the subgenual cingulate cortex reflects decreased emotional aversion to harming in counterintuitive utilitarian judgment. Cognition 126, 364–372. https://doi.org/10.1016/j.cognition.2012.11.002

Yamagishi, T., Takagishi, H., Fermin, A. de S.R., Kanai, R., Li, Y., Matsumoto, Y., 2016. Cortical thickness of the dorsolateral prefrontal cortex predicts strategic choices in economic games. Proc. Natl. Acad. Sci. 201523940. https://doi.org/10.1073/pnas.1523940113

Yankouskaya, A., Humphreys, G., Stolte, M., Stokes, M., Moradi, Z., Sui, J., 2017. An anterior–posterior axis within the ventromedial prefrontal cortex separates self and reward. Soc. Cogn. Affect. Neurosci. 12, 1859–1868. https://doi.org/10.1093/scan/nsx112

Zaki, J., Mitchell, J.P., 2011. Equitable decision making is associated with neural markers of intrinsic value. Proc. Natl. Acad. Sci. 108, 19761–19766. https://doi.org/10.1073/pnas.1112324108

Zanon, M., Novembre, G., Zangrando, N., Chittaro, L., Silani, G., 2014. Brain activity and prosocial behavior in a simulated life-threatening situation. Neuroimage 98, 134–146. https://doi.org/10.1016/j.neuroimage.2014.04.053

Zheng, H., Zhu, L., 2013. Neural mechanism of proposer's decision-making in the ultimatum and dictator games. Neural Regen. Res. 8, 357–62. https://doi.org/10.3969/j.issn.1673-5374.2013.04.008