When Your Outcomes Become My Rewards: Individual Differences in the Neural Representation of Others' Outcomes Drives Prosociality (or Antisociality)

by

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Abstract

Contemporary theories of prosociality suggest the mesolimbic dopamine reward circuit may play a critical role in enabling prosociality during social decision-making. One implication is that people who find good outcomes for others to be rewarding should incorporate this signal during decision-making, and variance in the strength of this signal should lead to variations in decision-making. The degree to which others' outcomes were experienced as rewarding was estimated through the modelling of outcome-period BOLD activity in a social decision-making task. Variation in reward to others' outcomes moderated decision-making and related to established metrics of empathy, suggesting that the degree to which others' outcomes will be rewarding to the self are incorporated during decision-making. The ability of the reward system to represent others' outcomes may be an exaptation of the reward system in hypersocial animals, though, how others' outcomes are represented in the reward system can promote either prosocial or antisocial behaviour.

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1 Introduction

One prominent group of contemporary models proposes that the mesolimbic dopaminergic reward system may have a critical role in enabling prosociality during social decision-making (e.g. Fehr & Camerer, 2007; Zaki & Mitchell, 2013; Hutcherson et al., 2015). This reward system, which guides the pursuit of primary rewards such as the pursuit of food when we are hungry, may also have the ability to represent how good or bad an outcome may be for another person. Good outcomes for others may thus be pursued and reinforced like a primary reward, allowing for an overlap in reward representations of the self and others.

In the same way we have strong affective associations with the pursuit of food, like feeling bad when hungry, and the enjoyment during and after eating, close relationships between the mesolimbic reward circuit and affect (e.g. Bechara, Damasio, Damasio, & Anderson, 1994) suggest that reward-based representations of others may be a bridge which can connect outcomes influencing another to our own affective experience. Through such a mechanism, simply pursuing what promotes positive affect for the self may thus lead to prosocial behaviour. This mechanism may represent an elegant and efficient exaptation of the reward system in hypersocial animals such as humans. This mechanism may then possibly form the basis for our affective/bodily-based forms of empathy such as experience sharing (Zaki & Ochsner, 2012) or "feeling with" (Decety and Jackson, 2004; de Vignemont and Singer, 2006).

Such models of prosociality are primarily supported by convergence between three groups of findings. First, these models need to contain at least one point where the subjective value of other-related information or more abstract concepts can be represented. Neuroimaging research has robustly demonstrated that the value of secondary rewards like money are represented within the mesolimbic circuit in regions like the orbitofrontal cortex (OFC; e.g. Knutson, Fong, Adams, Varner, & Hommer, 2001; O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001). Evidence of more abstract, social reward representation within the mesolimbic dopamine circuit has also been observed, such as when witnessing another win money (Mobbs et al., 2009), witnessing fair outcomes (Tricomi, Rangel, Camerer, & O'Doherty, 2010), or donating to charities (Hare, Camerer, Knoepfle, O'Doherty, & Rangel, 2010; Moll et al., 2006).

Second, these models require a point where disparate value representations can be directly compared. Computational modelling of the ventromedial prefrontal cortex (VMPFC) suggests this region houses a function which converts value calculations to a common currency or scale, allowing for the comparison of primary, secondary, and more abstract value representations within the circuit (Montague & Berns, 2002). Research suggests this comparison process is completed through an attractor neural network to determine which representation(s) have greatest value (Grabenhorst & Rolls, 2011).

Lastly, the existence of this comparison process between choice options suggests that value representations related to others or abstract social concepts should overlap with value representations related to more primary or self-focused rewards in the VMPFC. When making choices for the self and an other, activity tracking fairness-related value closely neighboured that of self-related value in areas of the VMPFC (Zaki & Mitchell, 2011). Computational modelling of choices for the self and an other then revealed directly overlapping regions of the VMPFC tracking the representation of self- and other-related value (Hutcherson, Bushong, & Rangel, 2015; Hutcherson & Tusche, 2018).

One implication of these models of prosociality is that people who find good outcomes for others to be rewarding should incorporate this signal during decision-making, and variance in the strength of this signal should lead to variations in decision-making. Previous work has hinted at this connection. Computational models of decision-making have estimated individual-level variability in the value attached to other-related information and these estimates have correlated with reward activity during decision-making (Hutcherson et al., 2015). Reward signals during outcome processing were then able to distinguish choices made by mistake from those that were preferred, with greater reward activity at outcome when accidental choices were switched relative to when preferred choices were switched. The extent to which others' outcomes were experienced as rewarding is one possible source of variance that composed these estimates of other-related value, though this hypothesis has not yet been directly tested.

If study design ensures orthogonality of BOLD value signals at decision- and outcome-periods, modelling parametric relationships between outcome-period reward activity and self and other outcomes should capture the degree to which other's outcomes are rewarding. Confounding motivational factors related to social desirability, norms, or demand characteristics often shape behaviour. However, modelling outcome-period value processing can tease apart prosocial behaviour motivated by such confounds from prosocial behaviour motivated by reward coding of others' outcomes. For example, if prosocial behaviour is driven by reward coding of others' outcomes, information related to others' outcomes will be of interest during both the decision-period and outcome period (making decisions that influence others' outcomes and observing the outcomes themselves). Alternatively, if prosocial behaviour is driven by motivations related to social norms, such as wishing to avoid judgement that could result from behaving too selfishly, motivations to attend to other-related information at the outcome period should be minimal as the required prosocial behaviour was completed during the decision-period. Estimation of relationships between reward and others' outcomes during the outcome period would then allow for investigations of the impact this input has on decision-making.

The current work isolates outcome-period reward activity in an fMRI social-decision making task, the Dual Gamble task, in an attempt at capturing the degree to which other's outcomes are rewarding. The nature of this variable is examined through comparisons with established measures of individual differences such as empathy. This variable is then used to test the hypothesis that people who find good outcomes for others to be rewarding should incorporate this signal during decision-making in the decision-period of the task, and that variance in the strength of this signal should lead to variations in decision-making.

2 Methods

2.1 Participants

51 right-handed participants were recruited for participation from The Ohio State University and surrounding community. All participants had no current or previous history as a person surviving with mental health challenges, no reported neurological history, and normal or corrected-to-normal vision. Two participants were excluded from analysis due to technical issues, leaving a final count of 49 participants used during analysis (26 female; age_{mean}= 22.80, age_{range}= 18-43). The entire session lasted an average of 1.5 hours and participants were paid $20 USD for their time, plus any self-related gamble winnings and any winnings from the gambling decisions of the participant with which they were paired. The fixed compensation and self-related gamble winnings were paid out immediately at the end of the study, while participants were then contacted within the following two weeks about any additional money they were due from the decisions of the participant with which they were paired and arrangements were made for participants to pick up the winnings. No deception was used in the study.

2.2 The Dual Gamble Task

In the Dual Gamble task, participants made gamble decisions simultaneously for themselves and an unknown other participant who they were paired with. On each trial, participants saw a screen depicting two gambles, with one gamble for the self and a second gamble for the other participant. The gambles were always presented on the same side (counterbalanced across participants), such that if the gamble for the self was on the left side of the screen in the first trial, it was on the left side of the screen for all further trials.

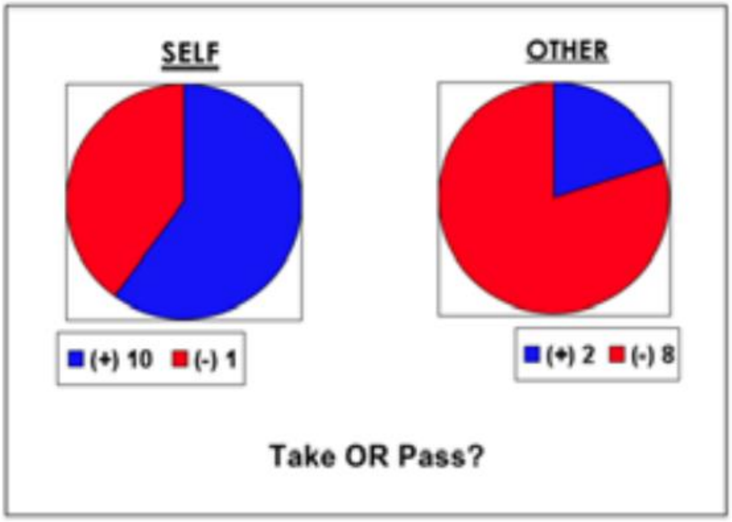
Each gamble contained three pieces of information: the probability of winning the gamble, the amount that would be won, and the amount that would be lost. For example, a participant may encounter a trial where the gamble for the self has a 60% chance of winning 10 points and a 40% chance of losing one point. They may then see that the gamble for the other has a 20% chance of winning 2 points and an 80% chance of losing 8 points. The details of each trial were communicated through pie chart illustrations and numbers (see Figure 1.), which participants mastered through practice before scanning. Probabilities and values were selected randomly and independently on each trial. Gamble win and loss values were selected randomly and independently on each trial from eight possible values: +/-10, +/-7, +/- 4, and +/-1. Win/loss probabilities were similarly selected randomly and independently on each trial from four possibilities: 80%/20%, 60%/40%, 40%/60%, and 20%/80%. Expected value and resulting outcomes were orthogonal for both self and other across trials, allowing for independent BOLD estimation.

The gambles were presented on-screen until participants made a button-response, with a timeout of five seconds. A fixation cross then appeared for four seconds before the outcome of each gamble was presented after an inter-trial fixation cross presented randomly for four, six, or eight seconds (ITI_{mean} = six seconds). Outcomes consisted of two numbers, with one indicating the outcome of the gamble for the self and one indicating the outcome of the gamble for the other (see Figure 2.). Critically, temporal separation of decision and outcome periods allowed for the independent modelling of decision- and outcome-related BOLD signal. Value processing for self and other at decision and outcome could thus each be independently estimated due to the previously mentioned orthogonality of expected value and outcome at decision and outcome.

The outcomes were presented onscreen for a total of four seconds, with no button-press response required or accepted from participants. Placement of self and other outcomes on the left or right side of the screen was always the same across trials, and matched the side which the gambles appeared on.

Figure 1

Exemplar trial from the Dual Gamble task.



Note. The area within a chart indicated the probability of each outcome while numbers below the pie chart communicated the value of each outcome. In this trial, the self-gamble had a 60% chance of winning 10 or a 40% chance of losing 1, while the other-gamble had a 20% chance of winning 2 and an 80% chance of losing 8. Participants had to make one decision, they could not choose between gambles but had to either take or pass both gambles together.

Figure 2.

Structure of the Dual Gamble task for fMRI scanning.

When evaluating gambles, participants had to make a single decision, they could not choose between gambles but had to either take or pass both gambles together. The outcomes of gambles that participants chose to take were added to their total points. The outcomes of gambles that participants chose to pass were not added to their points totals. Gamble outcomes were presented regardless of whether the gamble was taken or passed.

Making a single decision to accept or reject both gambles may be relatively easy on some trials, such as when both gambles are attractive (accept) or when both gambles are unattractive (reject). However, the relative weighting of self-interest and concern for the other can be explored when the decision is not obvious. When conflicting information was present, participants needed to weigh the relative benefit or cost to self and other to make their decision. Participants had the opportunity to forego opportunities for themselves if the costs were too high for the other, or to take on risk to allow an opportunity for another player.

2.3 Practice And Study Sessions

To ensure participants understood the design, they completed a practice session before entering the scanner (see practice session section below). Participants first did 20 practice trials before going into the scanner. The first ten practice trials did not have a time limit, and the second ten practice trials required that participants respond within five seconds, making it equivalent to the study in the scanner. Participants were informed that their outcomes in the practice trials would not affect their final outcomes in any way. The orientation of the practice trials (i.e. self gamble on the left side or right side of the screen) matched the orientation of the real decision task. Practice trials were completed immediately prior to scanning. During fMRI scanning, participants were then presented with 18 gambles per fMRI run, and completed six fMRI runs, for a total of 108 gambles per participant.

2.4 Questionnaires and Demographics

Personality and demographics questionnaires were randomly given either before scanning (before the practice trials) or after scanning. Questionnaires included the Toronto Empathy Questionnaire (TEQ; Spreng, McKinnon, Mar, & Levine, 2009) and the Levenson Self-Report Psychopathy Scale (LSRP; Levenson, Kiehl, & Fitzpatrick, 1995).

On the TEQ, participants respond to 16 items on a five-point scale (ranging from 0 – 4) asking how frequently they feel or behave in the way described. The scale response options are “never”, “rarely”, “sometimes”, “often”, and “always”. Sample items include “I enjoy making other people feel better”, and “I am not really interested in how other people feel” (reverse coded). Higher scores on the TEQ indicate more frequently feeling or behaving in the way described and thus higher levels of empathy.

The LSRP was designed to be a measure of psychopathy in non-incarcerated samples. Participants respond to 26 items on a four-point scale that contains “disagree strongly,” “disagree somewhat,” “agree somewhat,” and “agree strongly.” Sample items include “for me, what’s right is whatever I can get away with,” and “people who are stupid enough to get ripped off usually deserve it.” The LSRP can be split into primary and secondary psychopathy, with primary psychopathy reflecting a lack of empathy, and secondary psychopathy reflecting an inability to control one’s impulses (Levenson et al., 1995). Higher scores on the LSRP indicate more agreement with the items, and thus higher levels of psychopathy.

2.5 fMRI Acquisition

Scanning was conducted using a Siemens 3T Trio functional magnetic resonance imaging (TIM) system at The Center for Cognitive and Behavioral Brain Imaging (CCBBI) at The Ohio State University. Functional images were acquired in 34 axial slices parallel to the to the AC-PC line, and nearly isotropic functional images were acquired from inferior to superior using a single-shot gradient echo planar pulse sequence (3.33 mm thick; TE = 25 ms; TR = 2000 ms; in-plane resolution = 3 mm x 3 mm; matrix size = 64 x 64; FOV = 260 mm). The first five volumes of each run were discarded to allow for T1 equilibration effects. Following functional imaging, a high resolution T1-weighted anatomical image (MPRAGE; 60 sagittal slices; TE = 4.73 ms, TR = 1900 ms; resolution = 0.9×0.9×1.2 mm) was collected for normalization.

2.6 fMRI Preprocessing

fMRI Expert Analysis Tool (FEAT) Version 6.00, part of FSL (FMRIB’s Software Library, www.fmrib.ox.ac.uk/fsl) was used to perform brain extraction using BET (Smith, 2002), motion correction estimations with FSL’s MCFLIRT (Jenkinson, Bannister, Brady, & Smith, 2002), spatial smoothing with a Gaussian kernel with full-width at half-maximum (FWHM) of 6mm, and non-linear warping estimations with FMRIB's non-linear counterpart (FNIRT) using brain-based registration (Greve & Fischl, 2009), 12 degrees-of-freedom, and a non-linear warp resolution of 10mm. This FEAT output folder was fed into ICA-AROMA (Pruim, Mennes, Buitelaar, & Beckmann, 2015) for motion correction. The non-aggressive denoised functional outputs from ICA-AROMA for each run were warped to standard space and scaled to a common mean, before being taken to AFNI's 3dDeconvolve function (Cox, 1996).

Two independent deconvolutions of the functional fMRI were completed. First, to localize motivation in outcome BOLD signals, parametric modulation analyses were completed where outcome period self and other outcome magnitudes were modelled parametrically. Decision period self and other value magnitude were also modelled parametrically to control for decision-related value processing. Second, to extract decision-related BOLD for multi-level modelling of the decision process, each trial was modelled individually with LS-A (Mumford, Turner, Ashby, & Poldrack, 2012). BOLD activity to the outcome periods of each trial were also modelled with LS-A to ensure decision-related BOLD variance did not contain any outcome-related BOLD. In both deconvolutions, 3dDeconvolve's polynomial noise removal (POLORT) was set to automatic for removal of trends in the data.

3 Results

3.1 Behavioural Results

To examine the influence of self and other value on decision, responses (take or pass) were predicted using a multilevel logistic regression. Variables capturing self- and other-related information that predicted choice were computed as "expected value" (EV) variables for the Self and Other gambles as follows:

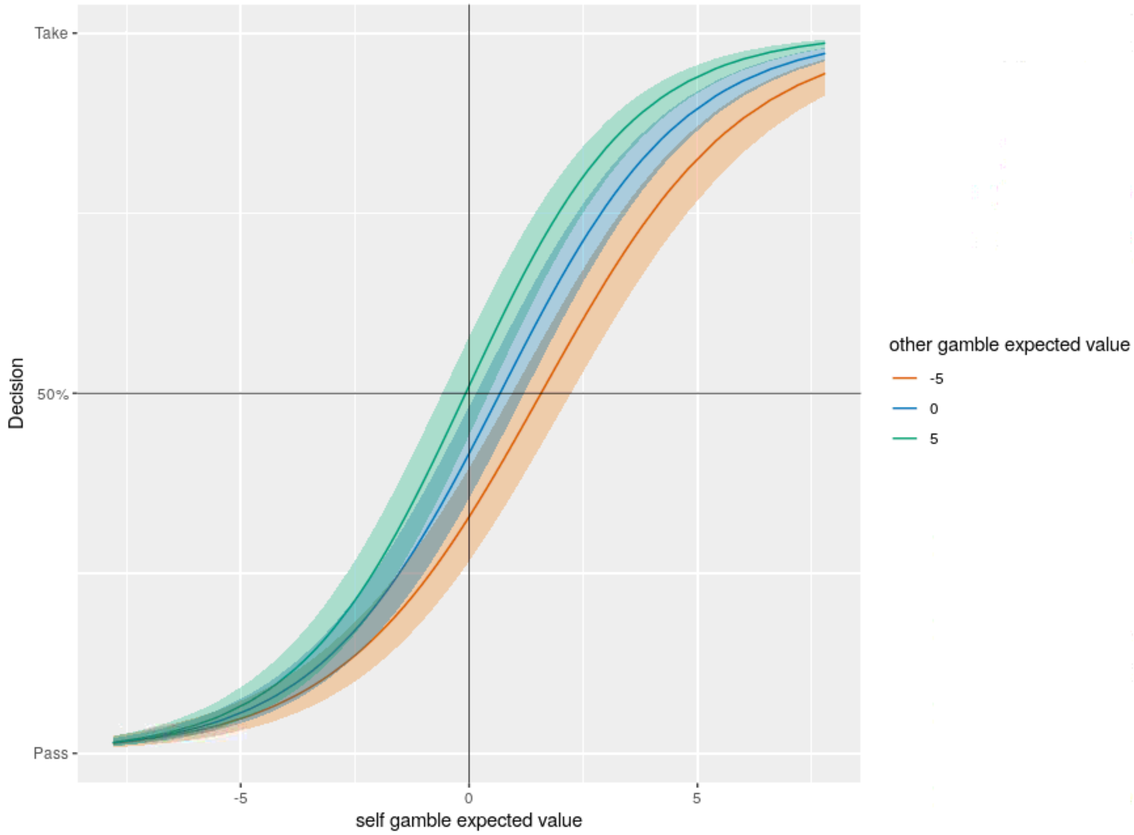
EV = (probability of winning) x (amount of possible points won) - (probability of losing) x (amount of possible points lost)

With these EV variables, decisions (take or pass) were modelled with multilevel logistic regression (using glmer from the "lme4" package in R) as a function of the expected value for the Self gamble (SelfEV), the expected value for the Other gamble (OtherEV), and the interaction between these variables (SelfEV × OtherEV), with trials nested within participants and runs.

Replicating previous work (Allidina et al., 2019; Arbuckle and Cunningham, 2012), positive main effects of SelfEV ($\beta = 0.497$, $p < 0.001$) and OtherEV ($\beta = 0.076$, $p < 0.001$) were observed on the decision to take a gamble, indicating that on average, people choose to take gambles that increased point totals for both themselves and others. The effect of SelfEV was larger than that of OtherEV, $\chi^2(1) = 186.79$, $p < 0.001$, indicating that, on average, self value is given higher priority than other-related value. As seen in Figure 3., the significant interaction between SelfEV and OtherEV on the decision to take a gamble ($\beta = 0.009$, $p = 0.031$) suggested that participants took OtherEV into account more when SelfEV was positive. A good gamble for the self was more likely to be taken when accompanied by a good gamble for the other, and a good gamble for the self was less likely to be taken when accompanied by a bad gamble for the other. The worse the gamble was for the self, the less OtherEV mattered for decision.

Figure 3

The interaction of self- and other-expected value (EV) on decision-making.



3.2 Neural Correlates of Value-Based Decision-Making

To examine neural correlates related to action-selection and value representation, the preprocessed functional data was separately modelled for the decision and outcome phases of each trial, with trials separated into those which participants took or passed on, resulting in four groups of onsets: 2 (decision or outcome period) by 2 (gamble during decision period was taken or passed).

Deconvolution of each set of onsets was completed using AFNI's 3dDeconvolve function (Cox, 1996). In addition to intercept modelling for each group of onsets, parametric modulations were modelled with "-stim_times_AM2". Decision-period intercepts were modulated by the previously computed expected value (EV) variables. Outcome period intercepts were modulated by the outcomes that resulted from the gamble. These regressors were convolved with "dmBLOCK(1)" function. Decision-phase regressors were duration-modulated by decision response time. Outcome-phase regressors were duration-modulated by a constant length of two seconds. Second-level analysis of the whole brain data was carried out using AFNI's 3DANOVA2 for the computation of contrast maps and one-way t-tests as described below.

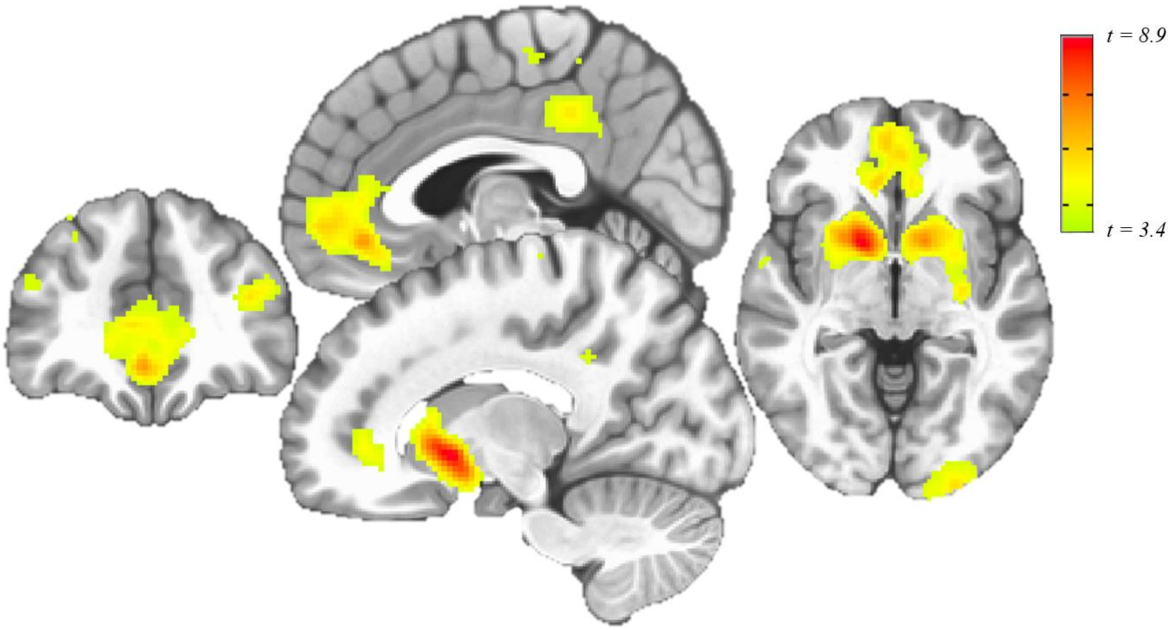
Trials on which no response was made before a five second timeout were modelled as junk trials with a duration of five seconds. The mean number of junk trials was 1.8% of trials (96 out of 5292). Minimum number of such trials across participants was 1/96 trials, maximum was 12/96 trials.

3.2.1 Neural Correlates of Value Representation

Self-related reward representation in mesolimbic dopamine regions has been robustly observed in neuroimaging research, with activity in regions such as in the VMPFC and vStr linearly increasing with subjective value (e.g. Knutson et al., 2001; Kable & Glimcher, 2007). The value of self-related outcomes in the current task strongly replicated such findings. Parametric relationships between self-related outcome value and BOLD activity was observed in regions including the VMPFC and vSTR (see Figure 4.).

Figure 4

BOLD parametric relationships to self-value at outcomes.



Note. Thresholding was determined with AFNI's 3dClustSim (version 18.0.5), with voxel-wise threshold $p < 0.001$ and cluster threshold $p < 0.05$, the acf option, first-nearest neighbor clustering, and two-sided thresholding. This corresponded to a cluster extent threshold of greater than 117 voxels at $p < 0.001$.

3.2.2 Self- and Other-Value Overlap in the VMPFC

Theories of common currency or common scale comparison processes suggest that overlap between self- and other-value representations should be observed within the VMPFC (Montague & Berns, 2002; Grabenhorst & Rolls, 2011). To locate such a region, a contrast-coded one-way ANOVA was computed where the parametric effects of both self-amount and other-amount were significantly greater than 0 for the outcomes of trials on which participants took the gamble. Participant was modeled as a nested random factor.

Regions involved in the processing of both self and other outcomes included many regions commonly observed in social decision-making, including the VMPFC (see Figure 5.) as well as bilateral vStr, bilateral posterior parietal cortices, and left temporoparietal junction (TPJ).

Thresholding was determined with AFNI's 3dClustSim (version 18.0.5), with voxel-wise threshold $p < 0.001$ and cluster threshold $p < 0.05$, the acf option, first-nearest neighbor clustering, and two-sided thresholding. This corresponded to a cluster extent threshold of greater than 117 voxels at $p < 0.001$. 3dFWHMx was used to determine average participant-level noise in the BOLD signal.

Figure 5

Ventromedial prefrontal cortex (VMPFC) cluster parametrically activated for both self- and other-related outcomes.

Note. Thresholding was determined with AFNI's 3dClustSim (version 18.0.5), with voxel-wise threshold $p < 0.001$ and cluster threshold $p < 0.05$, the acf option, first-nearest neighbor clustering, and two-sided thresholding. This corresponded to a cluster extent threshold of greater than 117 voxels at $p < 0.001$.

3.3 Individual Differences in Reward to Others' Outcomes

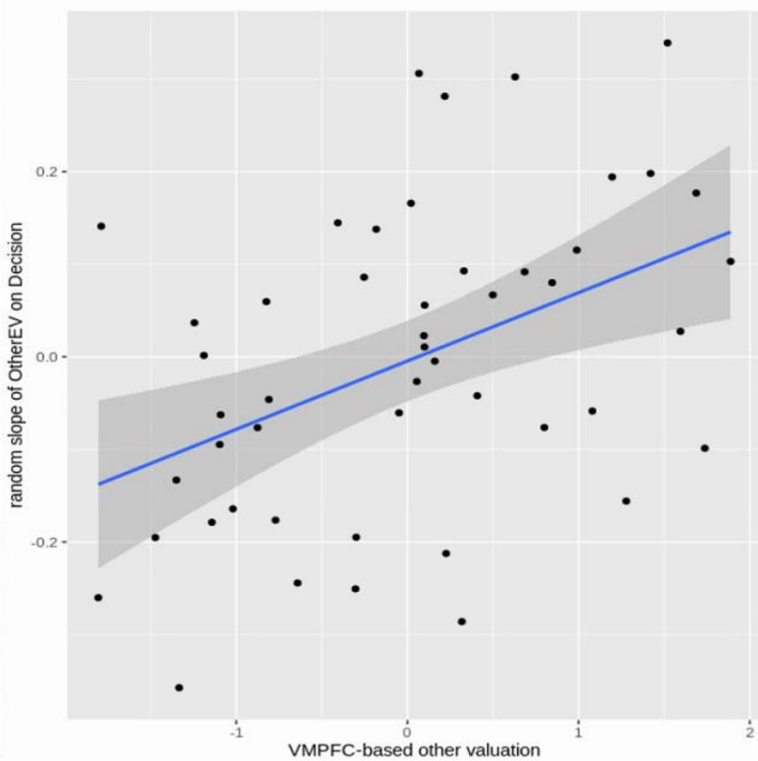
Having located a region of the VMPFC parametrically encoding both self- and other-related outcome values, the degree to which outcomes for the self or other were experienced as rewarding could then be calculated through examining the strength of the relationships between VMPFC BOLD and self or other outcome value as individual differences. If the reward-pursuit model of prosociality is supported, prosocial preferences and behaviour may manifest through differences in the reward value ascribed to prosocial or other-related information.Mean parametric modulation estimates within these regions across time were generated to provide regional participant-level slope estimates of the relationships between BOLD activity and self outcomes or other outcomes.

3.3.1 Reward to Others' Outcomes and Decision-Period Weighting of Others' Value

Computational models of decision-making have estimated individual-level variability in the value attached to other-related information and these estimates have correlated with reward activity during decision-making (Hutcherson et al., 2015). The extent to which others' outcomes were experienced as rewarding is one possible source of variance that composed these estimates of other-related value (see Figure 6.). VMPFC to others' outcomes correlated with estimated random slopes of the relationship between decision and otherEV during decision-making ($r(47) = .44$, $p = .001$). Higher values for the random slope between decision and otherEV indicate that increasing otherEV led to increasing choices to take the gamble. Correlations between this variable and VMPFC to others' outcomes suggests those who experienced greater reward to others' outcomes also weighed good outcomes for the other as more valuable during decision.

Figure 6

VMPFC-based other-valuation correlated with estimated random slopes of the relationship between decision and otherEV.



Note. Higher values for the random slope between decision and otherEV indicate that increasing otherEV led to increasing choices to take the gamble. Correlations between this variable and VMPFC to others' outcomes suggests those who experienced greater reward to others' outcomes also weighed good outcomes for the other as more valuable during decision.

3.3.2 Reward to Others' Outcomes Correlates with Self-Report Empathy and Psychopathy

The extent to which one represents other-related information within the mesolimbic circuit may be directly related to the extent to which other-related outcomes influence one's affective state. Thus, reward system coding of other-related information may be related to empathy, particularly experience sharing (Zaki & Ochsner, 2012) or “feeling with” (Decety and Jackson, 2004; de Vignemont and Singer, 2006).

To examine whether the VMPFC-based self-valuation and other-valuation scores contained variance captured by prominent scales measuring empathy, correlations between self-valuation and other-valuation scores were conducted with the Toronto Empathy Questionnaire (TEQ) and the Levenson Self-Report Psychopathy Scale (LSRP).

On the TEQ, participants answer how frequently they feel or behave in ways such as “I enjoy making other people feel better”, and “I am not really interested in how other people feel” (reverse coded). Higher scores on the TEQ indicate higher levels of empathy. The LSRP can be split into primary and secondary psychopathy, with primary psychopathy reflecting a lack of empathy, and secondary psychopathy reflecting impulsivity (Levenson et al., 1995).

Computing two-sided Pearson’s paired-samples correlations, other-valuation was moderately correlated with Toronto Empathy Questionnaire (TEQ) scores ($r(47) = .29$, $p = .043$). Furthermore, other-valuation was moderately negatively correlated with primary psychopathy from the LSRP ($r(47) = -.302$, $p = 0.035$; no relationship to secondary psychopathy, $p > .50$).

Partial correlations examining relationships between other-valuation and either TEQ or primary psychopathy scores while controlling for the other were not significant (both p’s > .25), suggesting the other-valuation is correlating with the same shared variance in both the TEQ and primary psychopathy correlations.

Lastly, self-valuation did not correlate with the TEQ or either the primary or secondary psychopathy measures from the LSRP (both p’s > .85).

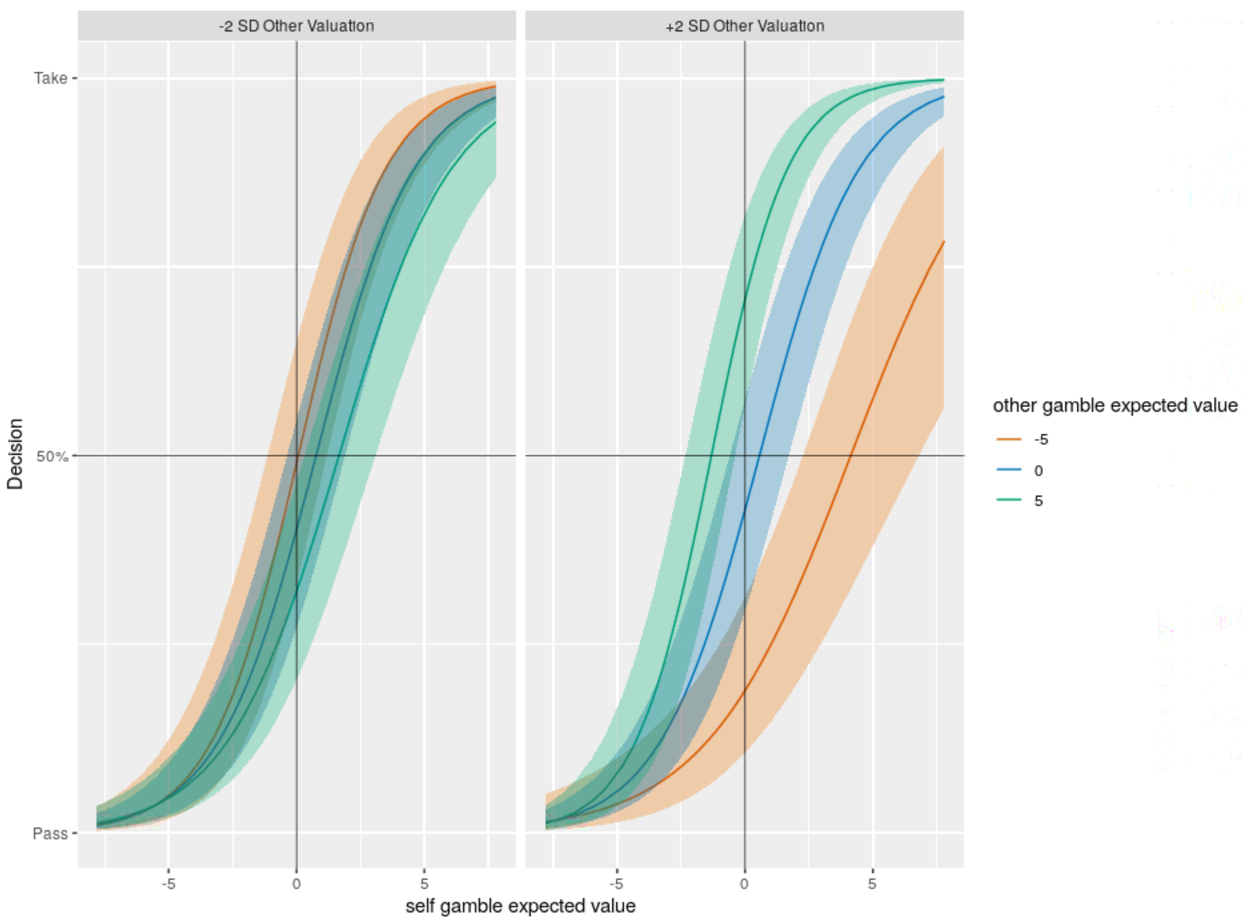
3.3.3 Reward to Others’ Outcomes Moderates Social Decision-Making

According to the reward-pursuit model of prosociality, the extent to which one’s mesolimbic circuit values the outcomes of the other should determine the extent to which one feels joy or loss at positive and negative outcomes for the other, and this experience should guide behaviour. To examine how variability in our VMPFC-based signals of self-valuation and other-valuation relate to behaviour during the decision-period of the task, decision modelling was moderated by the VMPFC self-valuation and other-valuation variables.

Decisions were modelled as a function of SelfEV, OtherEV, the interaction of SelfEV and OtherEV, and all terms were moderated by the VMPFC self-valuation and other-valuation variables, with random intercepts estimated within run and participant. As seen in Figure 7., the relationship between decision and the interaction of SelfEV and OtherEV was moderated by VMPFC-based other-valuation ($\beta = 0.011$, $t = 2.68$, $p = 0.007$). Specifically, those with higher other-valuation were more willing to take good gambles for the other, even at a cost to themselves, and less willing to take bad gambles for the other, again even at a cost to themselves. Meanwhile, those with the lowest levels of other-valuation were less willing to take good gambles for the self if they were also good for the other.

Figure 7

VMPFC-based other-valuation moderated the interaction of self- and other-expected value (EV) on decision.



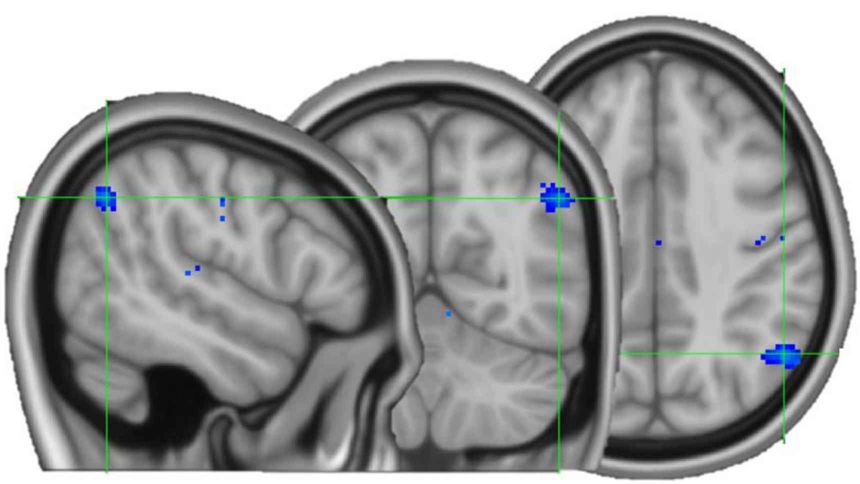
3.4 A Second Mechanism Supporting Prosociality

A second form of empathy, sometimes termed cognitive empathy, has been distinguished in the literature and this alternative mechanism has been linked to the functioning of separate regions such as the temporoparietal junction (TPJ) (e.g. Tusche et al., 2016). Self-other distinction and the performance of sociocognitive operations that require the representation of this distinction may be critically supported by the TPJ (Peckel, Kanske, & Singer, 2018; Lamm, Bukowski, & Silani, 2016; Quesque & Brass, 2019; Steinbeis, 2016). Thus, while the pursuit of others' outcomes for self-reward may enable prosociality, cognitive empathy and the TPJ may be particularly relevant to the promotion of prosociality when good for the other and good for the self do not share overlapping representation in the reward system.

Decisions were modelled as a function of SelfEV, OtherEV, the interaction of SelfEV and OtherEV, and voxel-wise trial-level fMRI with all terms moderated by VMPFC self-valuation and other-valuation variables, with random intercepts estimated within run and participant. Preliminary results revealed a higher-order 4-way interaction in the right TPJ (β = -0.037, t = -4.0, $p < 0.001$; See Figure 8.), suggesting that trial-level engagement of the rTPJ may promote prosociality particularly in the absence of reward to others' outcomes (see Figure 9). Significant clusters were also observed in the posterior parietal cortex, insula and parietal operculum, ventrolateral prefrontal cortex, and motor cortex.

Figure 8

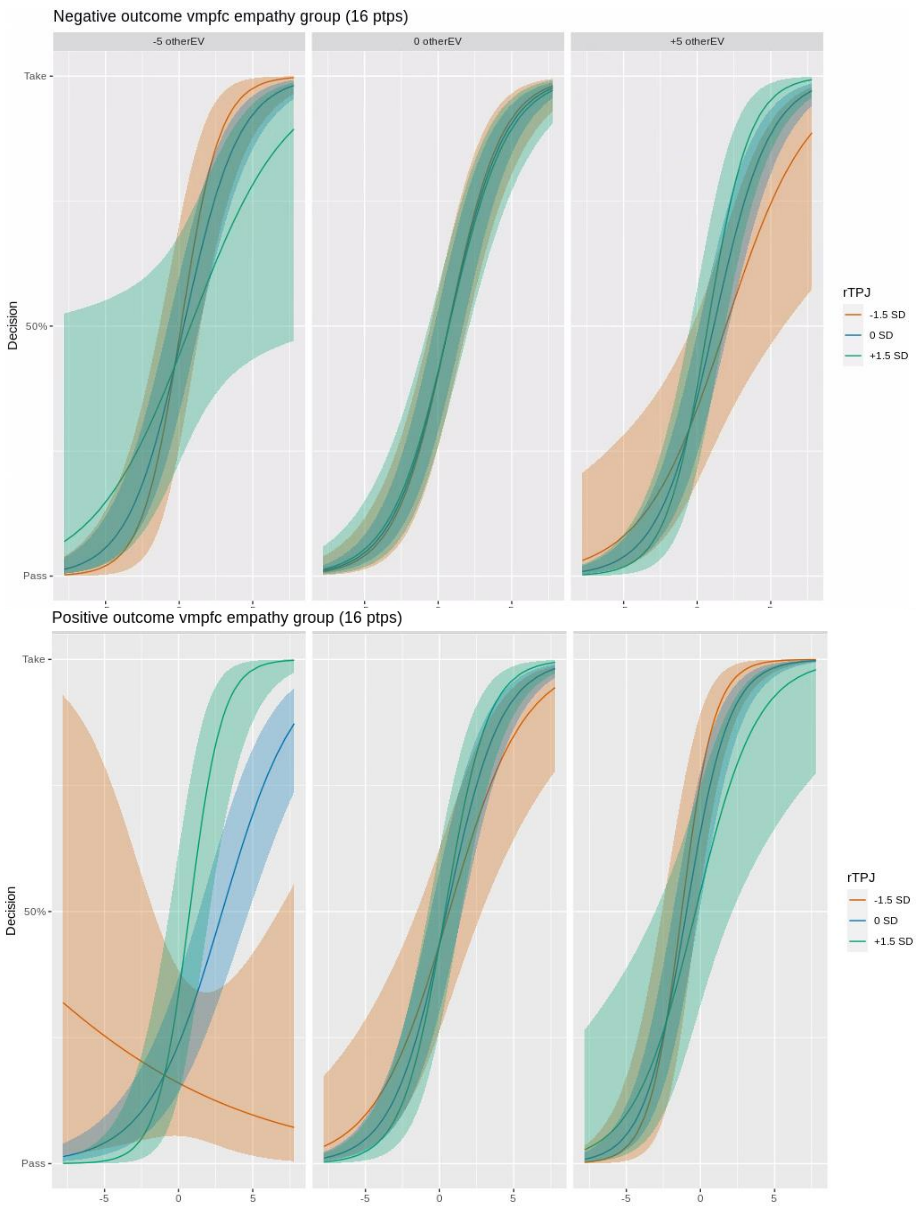
rTPJ cluster where trial-level activity supported prosociality in those with lower VMPFC-based reward to others' outcome.



Note. Thresholding was determined with AFNI's 3dClustSim (version 18.0.5), with voxel-wise threshold $p < 0.001$ and cluster threshold $p < 0.05$, the acf option, first-nearest neighbor clustering, and two-sided thresholding. This corresponded to a cluster extent threshold of greater than 117 voxels at $p < 0.001$.

Figure 9

Effects of trial-level rTPJ activity in those with positive and negative relationships to VMPFC-based other-valuation.



Note. Data subset into thirds by reward to others' outcomes for visualization purposes.

4 Discussion

Representing good outcomes for another as rewarding to the self could be a powerful mechanism for the promotion of prosociality. Such a mechanism would represent an elegant and efficient exaptation of the reward system in hypersocial animals, promoting prosociality through the simple pursuit of positive affect for the self. This mechanism could then possibly form the basis for our affective/bodily-based forms of empathy such as experience sharing (Zaki & Ochsner, 2012) or "feeling with" (Decety and Jackson, 2004; de Vignemont and Singer, 2006).

Previous work has hinted at this connection, with computational models of decision-making producing estimates of value attached to other-related information and these estimates have correlated with reward activity during decision-making (Hutcherson et al., 2015). Reward signals during outcome processing were then able to distinguish choices made by mistake from those that were preferred, with greater reward activity at outcome when accidental choices were switched relative to when preferred choices were switched. The extent to which others' outcomes were experienced as rewarding is one possible source of variance that composed these estimates of other-related value, though this hypothesis had not yet been directly tested.

The current work isolated the degree to which others' outcomes were experienced as rewarding through modelling of outcome-period reward activity to others' outcomes. Modelling individual differences in the extent to which good outcomes for the other were coded as rewarding, we created a variable representing the average relationship between activity in this region and how good the outcomes were for the other, for each participant. Some participants had positive relationships, suggesting that doing well for the other may have been encoded as rewarding. Some participants had no relationship, and some participants had negative relationships, suggesting that minimizing others' gains may have been experienced as more rewarding. Supporting these presuppositions, the reward to others' outcomes displayed moderate relationships with established self-report measures of empathy and psychopathy.

Since reward-based information is a key input signal into decision-making, the extent to which one represents good outcomes for the other as rewarding to the self should moderate our models of behaviour during the decision-period of the task. This was observed, with more positive relationships between reward activity and others' outcomes leading to prosocial outcomes such as increased willingness to take good gambles for the other and decreased willingness to take bad gambles for the other, even at a cost to the self. In contrast, more negative relationships led to decreased willingness to take good gambles for the other, even at a cost to themselves.

The current results suggest that the ability of the reward system to represent others' outcomes is one path that enables prosocial behaviour, though, how others' outcomes are represented in the reward system can promote either prosocial or antisocial behaviour. Models of intuitive prosociality hypothesize that evolutionary pressures for social living may have shaped humans to find prosociality automatically rewarding or rewarding by default (e.g. Zaki & Mitchell, 2013). The current results suggest that the human reward system is capable of promoting both prosociality or antisociality.

A second form of empathy, sometimes termed cognitive empathy, has been distinguished in the literature and this alternative mechanism has been linked to the functioning of separate regions such as the temporoparietal junction (TPJ) (e.g. Tusche et al., 2016). Self-other distinction and the performance of sociocognitive operations that require the representation of this distinction may be critically supported by the TPJ (Peckel, Kanske, & Singer, 2018; Lamm, Bukowski, & Silani, 2016; Quesque & Brass, 2019; Steinbeis, 2016). Thus, while the pursuit of others' outcomes for self-reward may enable prosociality, cognitive empathy and the TPJ may be particularly relevant to the promotion of prosociality when good for the other and good for the self do not share overlapping representation in the reward system.

The estimates of reward to others' outcomes used in the current work are unlikely to be completely free of confounding variance associated with alternative motivational factors. Judgements of moral character often involve consideration of both action and consequence (e.g. Cushman, 2008). If prosocial behaviour is driven by motivations related to social norms, such as wishing to avoid judgement that could result from behaving too selfishly, others' outcomes may still sometimes be attended to if simply behaving prosocially is not sufficient to assuage such concerns. One may feel motivated to ensure good outcomes for the other also occur, in addition to making a prosocial choice.

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