

Behavioral/Cognitive

Decomposing Gratitude: Representation and Integration of Cognitive Antecedents of Gratitude in the Brain

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Gratitude is a typical social-moral emotion that plays a crucial role in maintaining human cooperative interpersonal relationship. Although neural correlates of gratitude have been investigated, the neurocognitive processes that lead to gratitude, namely, the representation and integration of its cognitive antecedents, remain largely unknown. Here, we combined fMRI and a human social interactive task to investigate how benefactor’s cost and beneficiary’s benefit, two critical antecedents of gratitude, are encoded and integrated in beneficiary’s brain, and how the neural processing of gratitude is converted to reciprocity. A coplayer decided whether to help a human participant (either male or female) avoid pain at his/her own monetary cost; the participants could transfer monetary points to the benefactor with the knowledge that the benefactor was unaware of this transfer. By independently manipulating monetary cost and the degree of pain reduction, we could identify the neural signatures of benefactor’s cost and recipient’s benefit and examine how they were integrated. Recipient’s self-benefit was encoded in reward-sensitive regions (e.g., ventral striatum), whereas benefactor-cost was encoded in regions associated with mentalizing (e.g., temporoparietal junction). Gratitude was represented in perigenual anterior cingulate cortex (pgACC), the strength of which correlated with trait gratitude. Dynamic causal modeling showed that the neural signals representing benefactor-cost and self-benefit passed to pgACC via effective connectivities, suggesting an integrative role of pgACC in generating gratitude. Moreover, gyral ACC plays an intermediary role in converting gratitude representation into reciprocal behaviors. Our findings provide a neural mechanistic account of gratitude and its role in social-moral life.

Key words: cognitive antecedents; dynamic causal modeling; fMRI; gratitude; integration; reciprocity

Significance Statement

Gratitude plays an integral role in subjective well-being and harmonious interpersonal relationships. However, the neurocognitive processes through which various components and antecedents of gratitude are integrated remain largely unknown. We developed a new interpersonal paradigm to independently and parametrically manipulate two antecedents of gratitude in a helping context, namely, the benefit to beneficiary and the cost to benefactor, to examine their representation and integration in the beneficiary’s brain using fMRI. We found the neural encoding of self-benefit and benefactor-cost in reward- and mentalizing-related brain areas, respectively. More importantly, by examining effective connectivity, we showed that these componential signals are passed to perigenual anterior cingulate cortex, which tracks trial-by-trial gratitude levels. Our study thus provides a neural mechanistic account of gratitude.

Introduction

Gratitude is a typical social-moral emotion that plays a crucial role in maintaining human cooperative interpersonal relationship (McCullough et al., 2001; Haidt et al., 2004; M C T, 2004; L, 2004; K, 2014; M, 2015; M, 2015). Gratitude is represented in perigenual anterior cingulate cortex (pgACC), the strength of which correlated with trait gratitude (Haidt et al., 2003; A, 2009). T

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Materials and Methods

Participants

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Experimental design and statistical analyses

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Chau. The authors have received invaluable comments and suggestions concerning behavioral modeling and imaging analysis from discussions with these groups. We thank Joshua Brown for sharing the activation maps from Kini et al. (2016) for comparison; and Dr. Philip Blue for commenting on an earlier version of the manuscript. The authors declare no competing financial interests. *H.Y. and X.G. contributed equally to this work. Correspondence should be addressed to Dr. Xiaolin Zhou, School of Psychological and Cognitive Sciences Peking University, Beijing, 100871 China. E-mail: xz104@pku.edu.cn. DOI:10.1523/JNEUROSCI.2944-17.2018 Copyright © 2018 the authors 0270-6474/18/384887-13\$15.00/0

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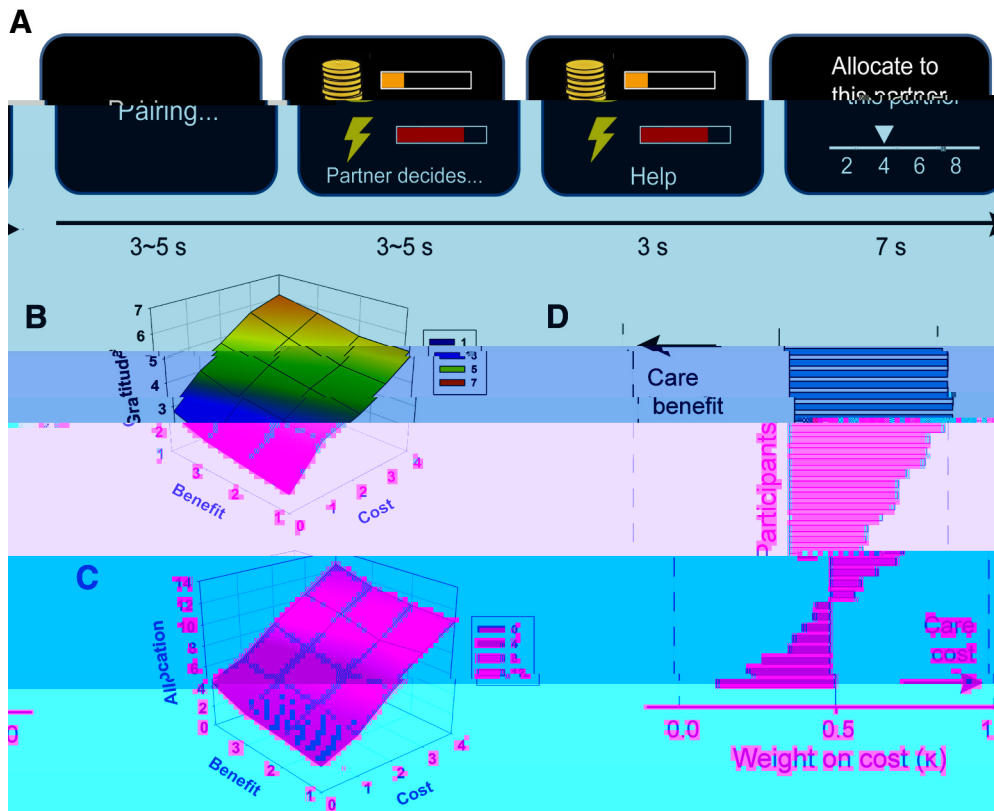


Figure 1. Experiment procedure and behavioral results. **A**, At the beginning of each trial, the participants were (anonymously and ostensibly) paired with 1 of 3 coplayers. Then the participants saw a pain-money pair and waited for the coplayer’s decision. If the coplayer chose Help, then the coplayer lost the corresponding amount of bonus while the participants would be exempted from the pain stimulation on this trial. If the coplayer chose NoHelp, then the coplayer could keep the bonus while the participants had to receive the corresponding pain stimulation. The presentation of the coplayer’s decision was defined as the critical events in the fMRI data analysis. At the end of the trial, the participant could allocate 20 Yuan (~\$3 U.S.) between himself/herself and the coplayer, with the knowledge that the coplayer was not aware of this procedure. **B, C**, Postscan gratitude rating and allocation during scanning (i.e., reciprocity) as a function of self-benefit and benefactor-cost. **D**, Relative weight of benefactor-cost over self-benefit in gratitude rating.

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Pain-money exchange task (behavioral). A

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Table 1. Distribution of NoHelp trials in different cost-benefit conditions

No. of NoHelp trials	Cost				
	0	1	2	3	4
Benefit 1	0	3	3	5	5
Benefit 2	0	3	3	4	5
Benefit 3	0	2	3	3	3
Benefit 4	0	1	2	3	3

The behavioral data were analyzed using a mixed-effects logistic regression model (GLM1) with benefit and cost as predictors. The model was fitted to the data using the maximum likelihood method (ML). The results showed that the probability of choosing the NoHelp option increased as the cost increased and as the benefit decreased. The interaction between cost and benefit was also significant, indicating that the impact of cost on the choice depends on the level of benefit. The model was compared to a null model (GLM2) using the Bayesian Information Criterion (BIC). The BIC for the null model was 111, and the BIC for the full model was 37, indicating that the full model provided a significantly better fit to the data. The results were also compared to a model that included only cost as a predictor (GLM3) and a model that included only benefit as a predictor (GLM4). The BIC for the null model was 111, the BIC for the cost-only model was 111, the BIC for the benefit-only model was 111, and the BIC for the full model was 37, indicating that the full model provided a significantly better fit to the data than any of the other models.

Analysis of the behavioral data. W

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fMRI data analysis. W MRI , 2

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cost were significant (benefit: 0.30 0.07, $t = 4.58$; cost: 0.80 0.16, $t = 5.02$); the interaction term did not reach significance ($\beta = 0.01$ 0.05, $t = 0.26$). For allocation (Table 3), the model with the two main effects was the best model. Parameters estimated based on this model showed that both benefit and cost were predictive of allocation (benefit: 0.64 0.10, $t = 6.11$; cost: 0.78 0.11, $t = 7.43$). Both gratitude rating and allocation increased monotonically with benefit and cost (Fig. 1B, C).

To examine whether the participants' allocation was influenced by trial history, namely, trial features (cost, benefit) and the benefactor's decision from the previous trial, we performed a separate regression model for allocation (Help trials alone) with this information included the following:

$$\text{Allocation}_{h,0} = \beta_1 \text{Cost}_{h,1} + \beta_2 \text{Benefit}_{h,1} + \beta_3 \text{Cost}_{h,1} + \beta_4 \text{Benefit}_{h,1} + \beta_5 \text{Decision}_{h,1} + \beta_6 \text{Decision}_{h,1} + \beta_7 \text{Cost}_{h,1} + \beta_8 \text{Decision}_{h,1} + \beta_9 \text{Benefit}_{h,1} \quad (2)$$

We found that the contribution of cost and benefit on the trial remained significant ($\beta_1 = 2.07$ 0.18, $t = 11.18$; $\beta_2 = 0.55$ 0.14, $t = 3.96$). Interestingly, the contribution of benefit on the last trial was also significant ($\beta_4 = 0.18$ 0.08, $t = 2.26$), and it was qualified by a significant interaction with benefactor's decision ($\beta_7 = 0.27$ 0.10, $t = 2.65$). These results indicate that the participants allocated more on the current trial if the benefit on the last trial was high and the benefactor chose "Help." Benefactor's sacrifice on trial₁ did not influence participants' allocation on trial_n, nor did its interaction with benefactor's decision. These findings shed light on how the impacts of different cognitive antecedents on gratitude and reciprocity persist and decay over time. Decisive conclusion in this regard is beyond the scope of the current study because this study was not designed to address the question; thus, it did not balance the distribution of cost, benefit, and benefactor's decision over time.

As a result, the distribution of NoHelp trials was not balanced across different levels of cost and benefit, neither was it matched with the Help trials (Table 1). Future studies are needed to reveal the cognitive and affective response to other's withdrawal of help.

Neural representation of gratitude
Directly examining the representation of gratitude required us to have for each participant a trial-by-trial measure of gratitude and perform a parametric regression against brain activity elicited by

fMRI results

Neural representations of cost and benefit

Our first aim was to examine how the brain encodes benefit and cost when receiving help. Contrasts corresponding to the main effect of benefactor-cost and self-benefit in the Help conditions were defined based on the regressors in GLM 1 (see Materials and Methods). As we predicted, the main effect of benefactor-cost (Contrast 1) revealed activations in dorsomedial PFC, precuneus, and bilateral TPJs, the regions implicated in empathy and mentalizing (Table 4 Fig. 2A). The main effect of self-benefit (Contrast 2) revealed activations in a network related to value representation, including the ventromedial PFC, bilateral VS, and dorsal striatum (Table 4 Fig. 3A). Regional activation patterns were extracted from our hypothesized ROIs for illustrative purposes (Figs. 2B, 3B). As a comparison, the same set of contrasts defined for the NoHelp trials revealed no suprathreshold activation at the brain areas revealed by the corresponding contrasts in the Help trials (Figs. 2A, 3A). It is worth noting, however, that the null effect of the NoHelp contrasts is not sufficient to demonstrate that the neural processes observed here are specific to receiving help. To demonstrate specificity, one needs to show "separate modifiability" (e.g., Woo et al., 2014) of two constructs (e.g., Help vs NoHelp), which is beyond the scope of the current study.

Because our primary interest here is the neurocognitive processes underlying receiving help and feeling grateful, we included the NoHelp conditions only as fillers.

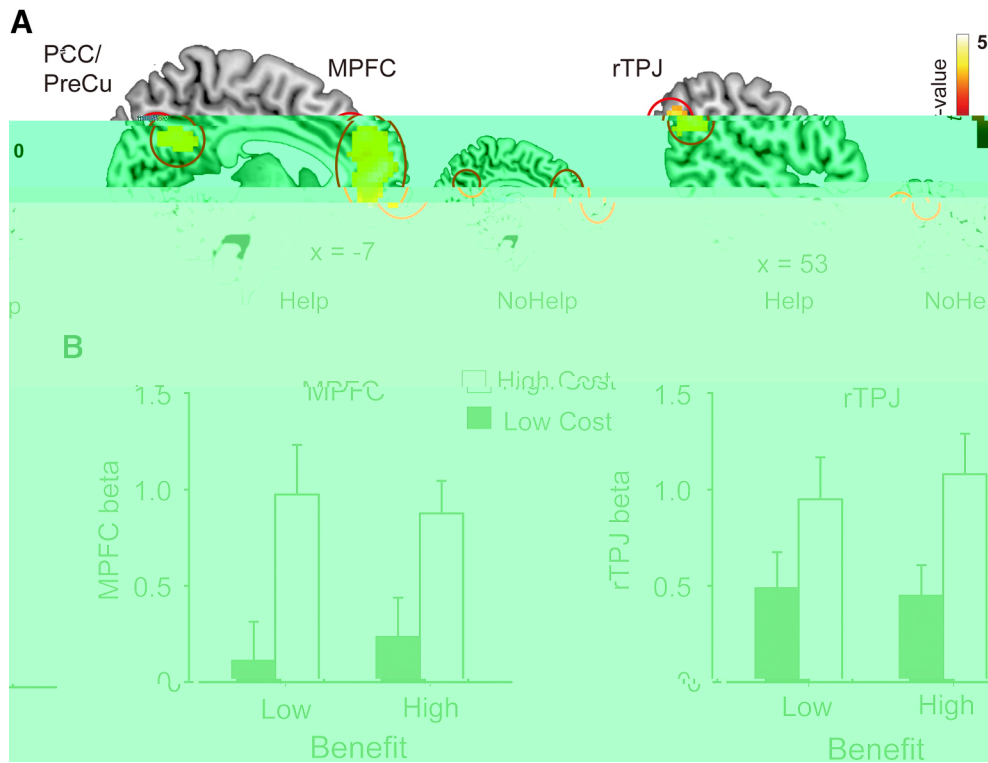


Figure 2. Encoding of benefactor-cost. **A**, Whole-brain contrast of high versus low cost in Help conditions (larger figure). The same contrast in the NoHelp conditions was inserted for comparison (smaller figure). **B**, Parameter estimates (β values) corresponding to the four Help conditions were extracted from MPFC and rTPJ for illustrative purposes. Error bars indicate standard error of means.

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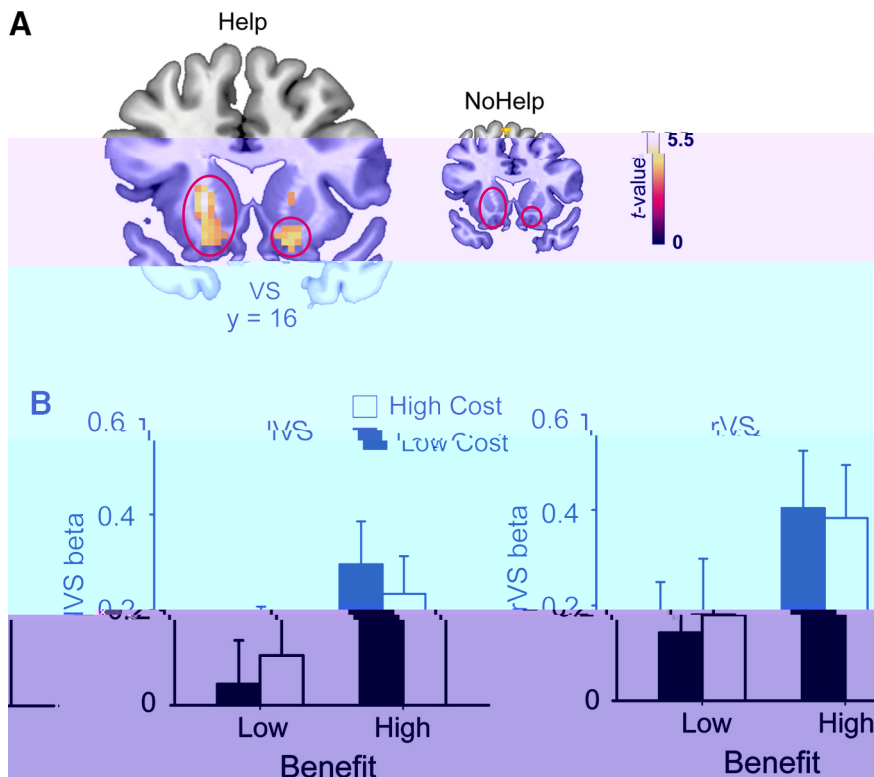


Figure 3. Encoding of self-benefit. *A*, Whole-brain contrast of high versus low benefit in Help conditions (larger figure). The same contrast in the NoHelp conditions was inserted for comparison (smaller figure). *B*, Parameter estimates (β values) corresponding to the four Help conditions were extracted from left VS and rVS for illustrative purposes. Error bars indicate standard error of means.

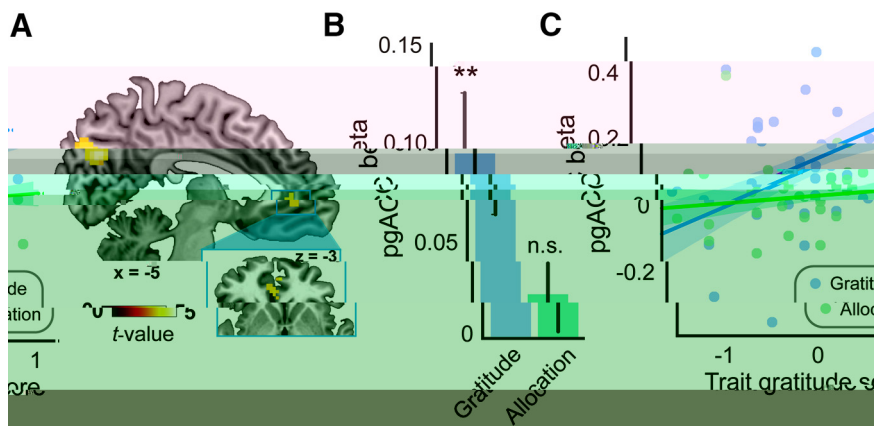


Figure 4. Representation of gratitude. *A*, Whole-brain parametric contrast of constructed gratitude. *B*, pgACC responses to constructed gratitude (blue) and allocation (green). *C*, Relation between trait gratitude score and pgACC responses to constructed gratitude (blue) and allocation (green). $**p < .005$. Error bars indicate standard error of means.

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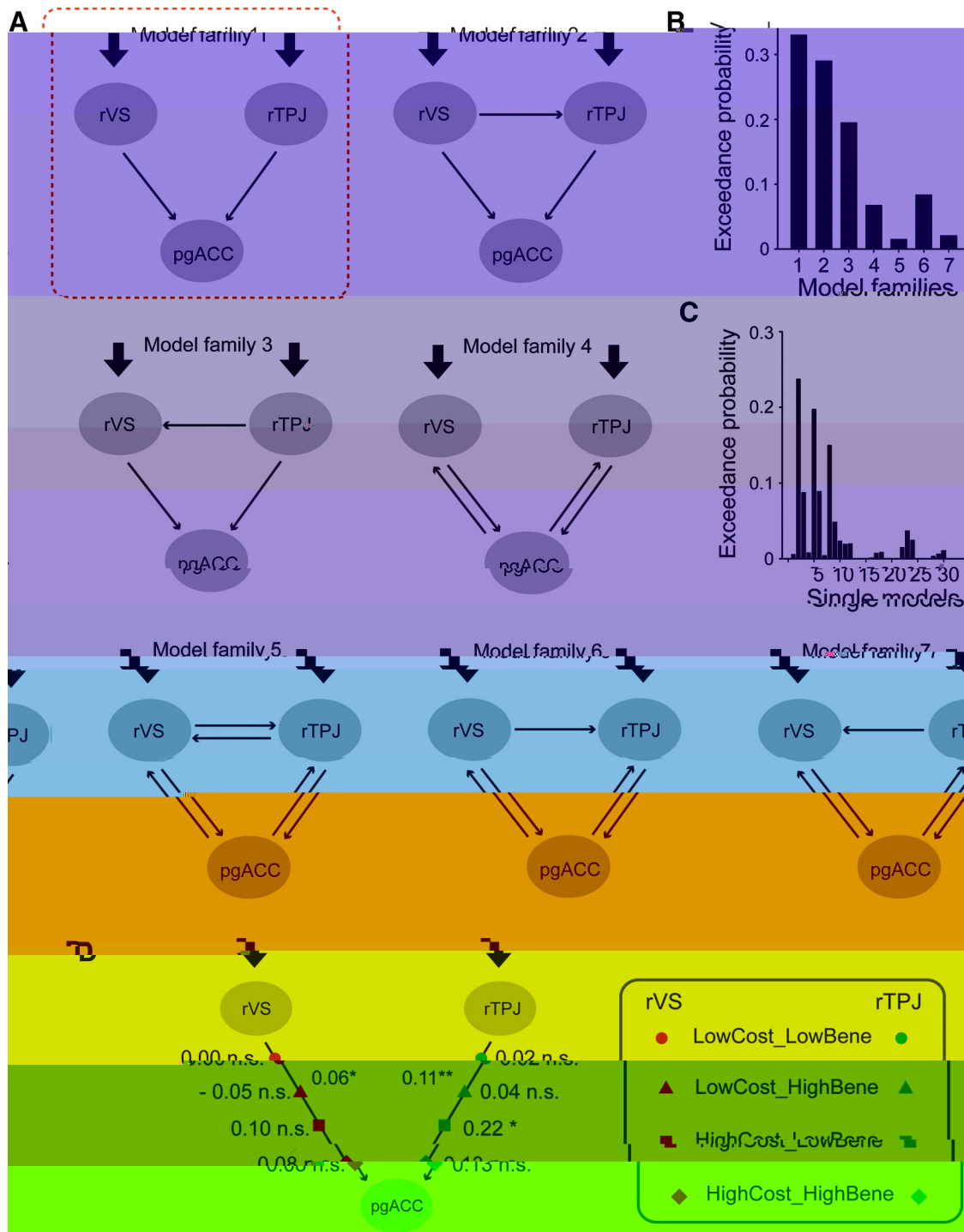


Figure 5. Results of effective connectivity (DCM) analysis. **A**, Thirty-three individual models, grouped into 7 model families, were constructed and compared using Bayesian Model Comparison. The exceedance probability of each family (**B**) and each individual model (**C**) are shown. Model Family 1, enclosed in the red square, has the highest exceedance probability. **D**, Strength of intrinsic and modulatory connectivities estimated based on the winning family. * $p < 0.05$, ** $p < .005$.

Discussion

Gratitude is a complex emotion that involves a network of brain regions, including the ventral striatum (VS), the right temporoparietal junction (rTPJ), and the posterior cingulate cortex (ACC). The VS is a key region for reward processing, and the rTPJ is involved in social cognition and theory of mind. The ACC is a central hub for emotion and decision-making. The present study used a Bayesian model comparison approach to identify the most parsimonious model of the effective connectivity between these regions during gratitude. The winning model (Model Family 1) suggests that the VS and rTPJ both exert direct influences on the ACC, with no direct connection between the VS and rTPJ. This model was supported by the highest exceedance probability across all model families and individual models. The strength of these connections varied across four cost/benefit profiles: LowCost_LowBene, LowCost_HighBene, HighCost_LowBene, and HighCost_HighBene. The HighCost_HighBene profile showed the strongest modulatory connectivity from the rTPJ to the ACC (0.22, $p < 0.05$), while the other profiles showed no significant differences. These findings provide a neural basis for the experience of gratitude and its modulation by cost and benefit.

Table 5. Model parameters estimated based on Model Family 1

Parameter	Mean ± SD
Intrinsic connectivity	
VS → pgACC	0.06 ± 0.14*
rTPJ → pgACC	0.11 ± 0.18**
Modulation on VS → pgACC	
LowCost_LowBene	0.00 ± 0.06
LowCost_HighBene	−0.05 ± 0.42
HighCost_LowBene	0.10 ± 0.30
HighCost_HighBene	0.08 ± 0.67
Modulation on rTPJ → pgACC	
LowCost_LowBene	0.02 ± 0.06
LowCost_HighBene	0.04 ± 0.39
HighCost_LowBene	0.22 ± 0.59*
HighCost_HighBene	0.13 ± 0.60
Driving input to VS	
Help decision	0.04 ± 0.08*
Driving input to TPJ	
Help decision	0.06 ± 0.15*

VS, ventral striatum; TPJ, temporoparietal junction; pgACC, perigenual anterior cingulate cortex. * $p < 0.05$; ** $p < 0.005$.

Table 6. Functional connectivity (PPI) between rVS and rTPJ

Condition	Connectivity (mean ± SD)
LowCost_LowBene	1.51 ± 4.10
LowCost_HighBene	1.17 ± 2.69
HighCost_LowBene	1.44 ± 3.25
HighCost_HighBene	1.83 ± 4.95

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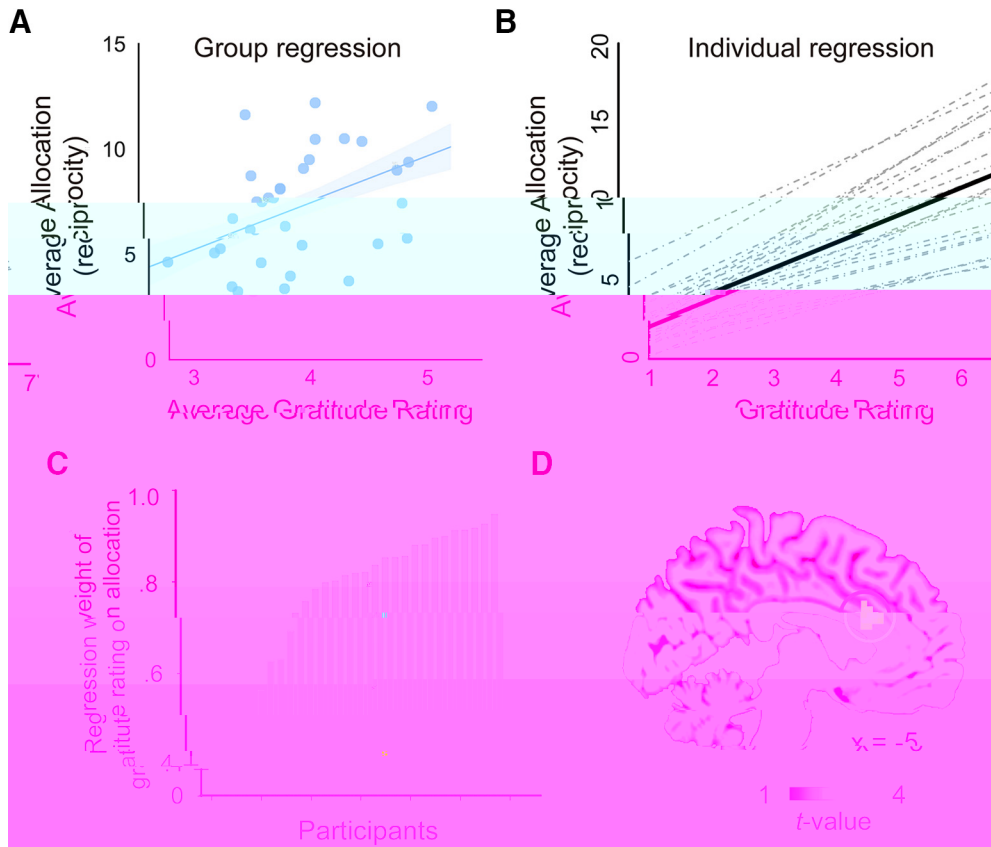


Figure 6. From gratitude to reciprocity. **A**, Average gratitude rating in the postscan gratitude recall of an individual participant predicts average monetary allocation (i.e., reciprocity) of that participant. **B**, Within each individual, variation in gratitude ratings predicts variation in allocation. The correlation reported here is the correlation between the postscan gratitude ratings in each of the 20 Help conditions and the average amount of allocation in the 20 Help conditions. Each dotted line indicates the regression line of a single participant, Solid line indicates the group effect. **C**, Individual differences in the exchange rate between gratitude and reciprocity (i.e., the slopes of the dotted lines in **B**). **D**, Neural correlates of individual differences in the exchange rate. This map is thresholded with $p < 0.005$ for illustrative purposes.

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References

A SB (2012) F, S P, P C 6:455 469. C R

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A SB, H J, G SL (2008) B, E 8:425 429. C R M

A M, B D, L AR, F PT, S L, E SB (2015) D, B S F 220:1031 1049. C R M

A MA, R N (2014) T, JN 34:6190 6200. C R M

B DJ, L R, S C, T HJ (2013) R, JM L 68:255 278. C R M

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B RJ (2013) T, N R 14:786 799. C R M

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F NH (1993) T, C E 7:357 387. C R

F KJ, B C, F GR, M J, R E, D RJ (1997) P, N 6:218 229. C R M

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H J, L Y, Y Y, B PR, Y H, Z X (2017) H, 157:598 611. C R M

H L, Z L, C R, Y H, L H, M A (2015) T, H B M 36:4346 4360. C R M

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