Article

The psychological, computational, and neural foundations of indebtedness

Received: 7 October 2020

Accepted: 7 December 2023

Published online: 02 January 2024

Check for updates

Xiaoxue Gao $\mathbb{O}^{1,2} \boxtimes$, Eshin Jolly \mathbb{O}^3 , Hongbo Yu \mathbb{O}^4 , Huiying Liu⁵, Xiaolin Zhou $\mathbb{O}^{1,2,6} \boxtimes$ & Luke J. Chang $\mathbb{O}^3 \boxtimes$

Receiving a favor from another person may induce a negative feeling of indebtedness for the beneficiary. In this study, we explore these hidden costs by developing and validating a conceptual model of indebtedness across three studies that combine a large-scale online questionnaire, an interpersonal game, computational modeling, and neuroimaging. Our model captures how individuals perceive the altruistic and strategic intentions of the benefactor. These inferences produce distinct feelings of guilt and obligation that together comprise indebtedness and motivate reciprocity. Perceived altruistic intentions convey care and communal concern and are associated with activity in insula, ventromedial prefrontal cortex and dorsolateral prefrontal cortex, while inferred strategic intentions convey expectations of future reciprocity and are associated with activation in temporal parietal junction and dorsomedial prefrontal cortex. We further develop a neural utility model of indebtedness using multivariate patterns of brain activity that captures the tradeoff between these feelings and reliably predicts reciprocity behavior.

Giving gifts and exchanging favors are ubiquitous behaviors that provide a concrete expression of a relationship between individuals or groups^{1,2}. Altruistic favors convey concern for a partner's well-being and signal a communal relationship such as a friendship, romance, or familial tie³⁻⁵. These altruistic favors are widely known to foster the beneficiary's positive feeling of gratitude, which can motivate reciprocity behaviors that reinforce the communal relationship⁶⁻⁹. Yet in daily life, favors and gifts can also be strategic and imply an expectation of reciprocal exchanges, particularly in more transactive relationships^{2,4,5,10-12}. Accepting these favors can have a hidden cost, in which the beneficiary may feel indebted to the favor-doer and motivated to reciprocate the favor at some future point in time¹³⁻²¹. These types of behaviors are widespread and can be found in most domains of social interaction. For example, a physician may preferentially prescribe medications from a pharmaceutical company that treated them to an expensive meal^{22,23}, or a politician might vote favorably on policies that benefit an organization, which provided generous campaign contributions²⁴. However, very little is known about the psychological, computational and neural mechanisms underlying this hidden cost of indebtedness and how it ultimately impacts the beneficiary.

Immediately upon receipt of an unsolicited gift or favor, the beneficiary is likely to engage in a mentalizing process to infer the benefactor's intentions²⁵⁻²⁷. Does this person care about me? Or do they expect something in return? According to appraisal theory²⁸⁻³³, these types of cognitive evaluations can evoke different types of feelings, which will ultimately impact how the beneficiary responds. Psychological Game Theory (PGT)³⁴⁻³⁶ provides tools for modeling these higher order beliefs about intentions, expectations, and fairness in the context of reciprocity decisions^{26,27,37,38}. Actions that are inferred to be motivated by altruistic intentions are more likely to be rewarded,

¹Shanghai Key Laboratory of Mental Health and Psychological Crisis Intervention, School of Psychology and Cognitive Science, East China Normal University, Shanghai 200062, China. ²School of Psychological and Cognitive Sciences, Peking University, Beijing 100871, China. ³Department of Psychological and Brain Sciences, Dartmouth College, Hanover, NH 03755, USA. ⁴Department of Psychological and Brain Sciences, University of California Santa Barbara, Santa Barbara, CA 93106-9660, USA. ⁵Mental Health Education Center, Zhengzhou University, Zhengzhou 450001 Henan, China. ⁶PKU-IDG/McGovern Institute for Brain Research, Peking University, Beijing 100871, China. e-mail: xxgao@psy.ecnu.edu.cn; gxx114455@gmail.com; xz104@psy.ecnu.edu.cn; luke.j.chang@dartmouth.edu

while those thought to be motivated by strategic or self-interested intentions are more likely to be punished^{26,27,37,38}. These intention inferences can produce different emotions in the beneficiary³⁹. For example, if the benefactor's actions are perceived to be altruistic, the beneficiary may feel gratitude for receiving help, but this could also be accompanied by the feeling of guilt for personally burdening the benefactor⁴⁰⁻⁴³. Both feelings motivate reciprocity out of concern for the benefactor, which we refer to as "communal concern" throughout the paper^{44,45}. In contrast, if the benefactor's intentions are perceived to be strategic or even duplicitous, then the beneficiary is more likely to feel a sense of obligation^{13,14,21,46,47}. Obligation can also motivate the beneficiary to reciprocate^{13,14,21,46,47}, but unlike communal concern, it arises from external pressures, such as social expectations and reputational costs^{48,49} and has been linked to feelings of pressure, burden, anxiety, and resentment⁴⁹⁻⁵¹. Indebtedness has often been considered a unitary construct, defined singularly as either the feeling of guilt for personally burdening the benefactor⁴⁰⁻⁴³ or as a sense of obligation to repay^{13,14,21,46,47}. However, in everyday life, inferences about a benefactor's intentions are often mixed and we argue that indebtedness is a superordinate emotion that includes feelings of guilt for burdening the benefactor and social obligation to repay the favor.

In this work, we propose a conceptual model to capture how feelings of indebtedness arise and influence reciprocal behaviors (Fig. 1). Specifically, we posit that there are two distinct components of indebtedness—guilt and the sense of obligation, which are derived from appraisals about the benefactor's altruistic and strategic intentions respectively. The guilt component of indebtedness, along with

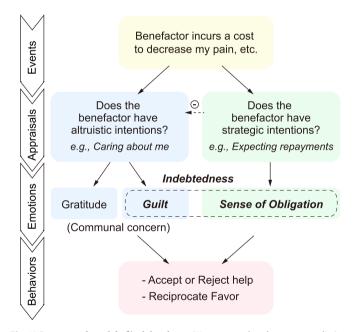


Fig. 1 | **Conceptual model of indebtedness.** We propose that there are two distinct components of indebtedness, guilt and the sense of obligation, which are derived from appraisals about the benefactor's altruistic and strategic intentions and can differentially impact the beneficiary's reciprocity behaviors. Following an event in which a benefactor provides help to the beneficiary (Yellow), the beneficiary is likely to appraise the benefactor's intentions. The higher the perception of the benefactor's strategic intention, the lower the perception of the benefactor's altruistic intention. The guilt component of indebtedness, along with gratitude, arises from appraisals of the benefactor's altruistic intentions (i.e., perceived care from the help) and reflects communal concern (Blue). In contrast, the obligation component of indebtedness results from appraisals of the benefactor's strategic intentions (e.g., second-order belief of the benefactor's expectation for repayment; Green). Both feelings of communal concern and obligation motivate the beneficiary's reciprocal behaviors (e.g., accept or reject the help and reciprocity after receiving help; Pink).

gratitude, arises from appraisals of the benefactor's altruistic intentions (i.e., perceived care from the help) and reflects communal concern. In contrast, the obligation component of indebtedness results from appraisals of the benefactor's strategic intentions (e.g., secondorder belief of the benefactor's expectation for repayment). Both feelings of communal concern and obligation motivate the beneficiary's reciprocal behaviors. We find support for this conceptual model in Study 1, in which participants describe memories of past emotional experiences in a large-scale online questionnaire, using regression analysis and topic modeling.

In Study 2, we move beyond self-report and focus specifically on how the guilt and obligation components of indebtedness arise and influence behaviors in the context of an interpersonal game. In this study, participants receive electrical shocks and anonymous benefactors (co-players) can choose to provide aid to the participants by spending money to reduce the duration of their pain experience. The participants, in turn, have the opportunity to accept or reject this help and also to reciprocate the benefactor's help by sharing some of their own money back. We experimentally manipulate the participants' beliefs about the benefactors' intentions by providing information about whether or not the co-players are aware that the participants have the opportunity to repay after receiving help. We find evidence supporting the hypothesis that appraisals of altruistic intentions produce guilt as well as gratitude (i.e., communal concern) while appraisals of strategic intentions lead to obligation. Building on previous models of other-regarding preferences^{37,38,52}, we develop computational models to predict reciprocity and help-acceptance decisions by quantifying the tradeoff between the latent motivations of self-interest, communal concern (consisting of guilt & gratitude), and obligation based on appraisals induced by the interpersonal task (Eq. 1).

In Study 3, we provide further validations of the conceptual model by examining the brain processes associated with the two components of indebtedness by scanning an additional cohort of participants playing the interpersonal game using functional magnetic resonance imaging (fMRI). We find that the processes of communal concern (i.e., guilt & gratitude) are associated with activity in the insula, ventromedial prefrontal cortex (vmPFC), and dorsolateral prefrontal cortex (dlPFC), while the processing of obligation is more associated with activity in the temporal parietal junction (TPJ) and dorsomedial prefrontal cortex (dmPFC). Finally, we construct a neural utility model of indebtedness by applying our computational model directly to multivariate brain patterns to demonstrate that neural signals reflect the tradeoff between these feelings and can predict participants' trialto-trial reciprocity behavior.

Results

Indebtedness is a mixed feeling comprised of guilt and obligation

In Study 1, we explore support for our conceptual model in selfreported experiences of Chinese participants collected via an online questionnaire. First, participants (n = 1619) described specific events, in which they either accepted or rejected help from another individual and rated their subjective experiences of these events. A regression analysis revealed that both self-reported guilt and obligation ratings independently and significantly contributed to increased indebtedness ratings ($\beta_{guilt} = 0.70 \pm 0.02$, 95%CI = [0.66, 0.73], t(1988) = 40.08, p < 0.001, $\beta_{\text{obligation}} = 0.40 \pm 0.02$, 95%Cl = [0.36, 0.44], t(1988) = 2.31, p = 0.021, linear regression, two-tailed, FDR corrected; Fig. 2a-I; Table S1). Second, participants were asked to attribute sources of indebtedness in their daily lives. While 91.9% participants stated that their feelings of indebtedness arose from feeling guilt for burdening the benefactor, 39.2% of participants reported feeling obligation based on the perceived ulterior motives of the benefactor (Fig. 2a-II; Fig. S1a). Third, participants were asked to describe their own personal definitions of indebtedness. We applied Latent Dirichlet Allocation (LDA)

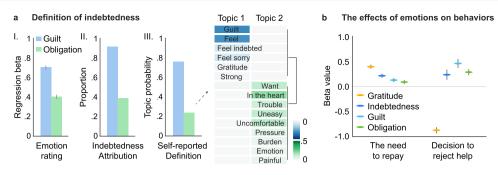


Fig. 2 | **Subjective experiences of indebtedness in Study 1. a** Contributions of guilt and obligation to indebtedness in Study 1 (n = 1619 participants). (I) Regression coefficients indicating the independent contributions of guilt and obligation ratings in predicting indebtedness ratings from recalling an event. Error bars reflect +/- SE of the estimate from the regression. (II) Proportion of participants attributing guilt and obligation as source of indebtedness. (III) Topic probabilities obtained from topic modeling of the emotional words in self-reported definition of indebtedness. Emotional words in each of the two topics extracted from self-

reported definition of indebtedness are listed in the right panel. The shade of background color underlying each word represents the probability of this word in the current topic. **b** The regression coefficients indicating the independent contributions of emotions on the self-reported need to repay after receiving help (n = 1598 help-acceptance events) and decisions to reject help (n = 1598 help-acceptance events). Data are presented as the regression coefficient +/– SE of the estimate from regression.

based topic modeling⁵³ to the emotion-related words extracted from the 100 words with the highest weight/frequency in the definitions of indebtedness based on annotations from an independent sample of raters (n = 80). We demonstrate that indebtedness is comprised of two latent topics (Fig. S1b, c). Topic 1 accounted for 77% of the variance of emotional words, including communal-concern-related words such as "guilt," "feel," "feel sorry," "feel indebted," and "gratitude". In contrast, Topic 2 accounted for 23% of the emotional word variance, including words pertaining to burden and negative bodily states, such as "uncomfortable," "uneasy," "trouble," "pressure," and "burden" (Fig. 2a-III). These results support the relationship between indebtedness and the feelings of guilt and obligation posited by our conceptual model.

Next, we examined how these distinct feelings relate to participants' self-reported responses to the help (Fig. 2b). Participants described events in which they chose to accept help and reported their experienced emotions. We found that self-reported indebtedness $(\beta = 0.20 \pm 0.04, 95\%$ Cl = [0.13, 0.27], t(1592) = 5.60, p < 0.001, linear regression, two-tailed, FDR corrected), guilt ($\beta = 0.12 \pm 0.04$, 95%Cl = $[0.04, 0.19], t(1592) = 2.98, p = 0.004), obligation (\beta = 0.09 \pm 0.04, 95\%)$ CI = [0.01,0.16], $t(1592) = 2.27, \quad p = 0.024),$ and gratitude $(\beta = 0.38 \pm 0.04, 95\%$ CI = [0.30, 0.45], t(1592) = 9.86, p < 0.001) all independently contributed to participants' reported need to repay after receiving help. Participants also described events, in which they chose to reject help and reported their anticipated counterfactual emotions had they instead accepted the benefactor's help⁵⁴. Decisions reject help were negatively associated with gratitude to $(\beta = -0.87 \pm 0.06, 95\%$ CI = [-0.99, -0.74], z(1986) = -13.65, p < 0.001,logistic regression, two-tailed, FDR corrected), but positively associated with indebtedness ($\beta = 0.23 \pm 0.10$, 95%Cl = [0.04, 0.42], z(1986) = 2.40, p = 0.017), guilt ($\beta = 0.46 \pm 0.09, 95\%$ Cl = [0.29, 0.65], z(1986) = 5.06, p < 0.001), and obligation ($\beta = 0.28 \pm 0.06$, 95%Cl = [0.16, 0.40], *z*(1986) = 4.70, *p* < 0.001). These results, based on subjective experiences, indicate that while gratitude, guilt, and obligation all contribute to reciprocating favors, only gratitude appears to be associated with increasing the likelihood of accepting help. The guilt and obligation components of indebtedness instead appear to be associated with increasing the likelihood of rejecting help.

Benefactor's intentions cause diverging components of indebtedness

We next sought to more specifically examine how indebtedness impacts behavior in the context of a laboratory-based task involving interactions between participants in Study 2a (n = 51, Fig. 3). In this

task, participants were randomly paired with a different anonymous same-gender co-player (benefactor) in each trial and were instructed that they would receive 20 s of pain stimulation in the form of a burst of medium intensity electrical shocks. The participant was informed that each benefactor had been endowed with 20 yuan (~\$2.7 USD) and made a decision about how much to spend from this endowment to reduce the duration of pain experienced by the participant (i.e., benefactor's cost) during a separate lab visit. Unbeknownst to the participant, each benefactor's cost was predetermined by a computer program (Table S2). After seeing how much money the benefactor chose to spend, the participant reported how much they believed this benefactor expected them to reciprocate (i.e., second-order belief of the benefactor's expectation for repayment). In half of the trials, the participant had to passively accept the benefactor's help; in the other half, the participant could freely decide whether to accept or reject the benefactor's help. Finally, at the end of each trial, participants decided how much of their own 25 yuan endowment (~\$3.4 USD) they wanted to allocate to the benefactor as reciprocity for their help. We experimentally manipulated participants' beliefs about the benefactors' intentions by providing additional information regarding the benefactors' expectations of reciprocation. Each participant was instructed that before making decisions, some benefactors knew that the participant would be endowed with 25 yuan and could decide whether to allocate some endowments to them as reciprocity (i.e., Repayment possible condition), whereas the other benefactors were informed that the participant had no chance to reciprocate after receiving help (i.e., Repayment impossible condition). In fact, participants could reciprocate in both conditions during the task. After the task, all trials were displayed again in a random order and participants recalled how much they believed the benefactor cared for them (i.e., perceived care), as well as their feelings of indebtedness, obligation, guilt, and gratitude in response to the help they received for each trial. To ensure incentive compatibility, five trials were randomly selected to be enacted and participants received the average number of shocks and money based on their decisions at the end of the experiment. We ran an additional version of this experiment (Study 2b, n = 57), in which we further systematically varied the exchange rate of how much it cost the benefactor to reduce the participant's duration of pain (i.e., help efficiency). However, we did not observe any significant interaction effect between efficiency and any of other experimental variables in Study 2b (Table S6) and chose to combine these two studies for all Study 2 analyses (n = 108, Table S3; see Supplementary Notes and Tables S4 to S6 for separate results).

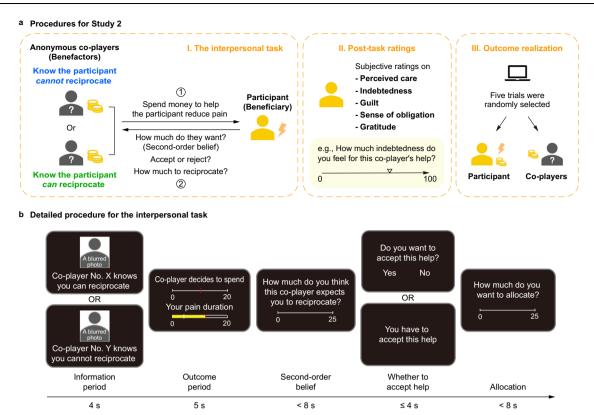


Fig. 3 | **Experimental procedures for Study 2. a** General procedures. In the interpersonal task (I), the participant was instructed that anonymous co-players (benefactors) made single-shot decisions to help reduce the duration of the participant's pain, and the participant, in turn, (1) reported how much they believed the benefactor expected them to reciprocate for their help (i.e., second-order belief), (2) decided whether to accept help, and (3) decided how much money to return to the benefactor. After the interpersonal task, participants recalled how much they believed the benefactor cared for them (i.e., perceived care), as well as their feelings of indebtedness, obligation, guilt, and gratitude in response to the help they received for each trial (II. Post-task ratings). At the end of the experiment, five trials in the interpersonal task were randomly selected to determine the participant's final amount of pain and payoff, and the selected benefactor's final payoffs (III. Outcome realization). **b** Detailed procedure for the interpersonal task. In each round, a different anonymous same-gender benefactor (represented by a blurred photo and a participant ID) decided how much of their endowment to

spend (i.e., benefactor's cost) to reduce the participant's pain duration. The more the benefactor spent, the more the duration of the participant's pain decreased. Participants indicated how much they thought the benefactor expected them to reciprocate (i.e., second-order belief). In half of the trials, the participant had to passively accept the benefactor's help; in the other half, the participant could freely decide whether to accept or reject the benefactor's help. Finally, at the end of each trial, the participant decided how much of their own endowment they wanted to allocate to the benefactor as reciprocity for their help. Unbeknownst to participants, benefactors' decisions (i.e., benefactor's cost) were pre-determined by the computer program (Table S2). We manipulated the perception of the benefactor knew the participant could (i.e., Repayment possible condition), or could not (i.e., Repayment impossible condition) reciprocate after receiving help. In fact, participants could reciprocate in both conditions during the task.

Our experimental manipulation successfully impacted participants' appraisals of the benefactors' hidden intentions behind their help. Participants reported increased second-order beliefs of the benefactors' expectations for repayment ($\beta = 0.53 \pm 0.03$, 95%Cl = [0.47, 0.59], t(107.04) = 15.71, p < 0.001, linear mixed model, twotailed) and decreased perceived care ($\beta = -0.31 \pm 0.02$, 95%Cl = [-0.35, -0.27], t(106.44) = -13.89, p < 0.001) (Fig. 4a, Table S3) when the participant believed the benefactor knew they could reciprocate (Repayment possible) compared to when they could not reciprocate (Repayment impossible). Both of these effects were amplified as the benefactor spent more money to reduce the participant's duration of pain (Fig. 4b, c, Table S3; second-order belief: $\beta = 0.22 \pm 0.02$, 95%CI = [0.18, 0.26], t(103.83) = 13.13, p < 0.001; perceived care: $\beta = -0.08 \pm 0.01$, 95%CI = [-0.10, -0.061t(98.59) = -6.64, p < 0.001). In addition, perceived care was negatively associated with second-order beliefs ($\beta = -0.44 \pm 0.04$, 95% CI = [-0.56, -0.32], t(89.56) = -11.29, p < 0.001) controlling for the effects of experimental variables (i.e., extra information about benefactor's intention, cost, and efficiency).

The belief manipulation not only impacted the participants' appraisals, but also their feelings. Our conceptual model predicts that

participants will feel indebted to benefactors who spent money to reduce their pain, but for different reasons depending on the perceived intentions of the benefactors. Consistent with this prediction, participants reported feeling indebted in both conditions, but slightly more in the Repayment impossible compared to the Repayment possible condition (Fig. 4a, Fig. S2a, Table S3, $\beta = -0.09 \pm 0.03$, 95%Cl = [-0.15, -0.03], t(105.81) = -2.98, p = 0.003). Moreover, participants reported feeling greater obligation ($\beta = 0.30 \pm 0.03$, 95%CI = [0.24, 0.36], t(106.82) = 9.28, p < 0.001), but less guilt ($\beta = -0.25 \pm 0.02$, 95% CI = [-0.29, -0.21], t(106.30) = -10.30, p < 0.001), and gratitude $(\beta = -0.27 \pm 0.02, 95\%$ Cl = [-0.31, -0.23], t(106.35) = -13.18, p < 0.001)in the Repayment possible condition relative to the Repayment impossible condition (Fig. 4a, Fig. S2b-d, Table S3). Similar to the appraisal results, these effects were magnified as the benefactor's cost increased (Fig. S2b-d, Table S3; obligation: $\beta = 0.11 \pm 0.01$, 95%Cl = [0.09, 0.13], t(100.74) = 8.85, p < 0.001; guilt: $\beta = -0.05 \pm 0.01, 95\%$ CI = [-0.07]-0.03], t(96.94) = -4.28, *p* < 0.001; gratitude: $\beta = -0.06 \pm 0.01$, 95%CI = [-0.08, -0.04], t(99.31) = -4.20, p < 0.001).

We conducted two separate types of multivariate analyses to characterize the relationships between appraisals and emotions. First, exploratory factor analysis (EFA) on the subjective appraisals

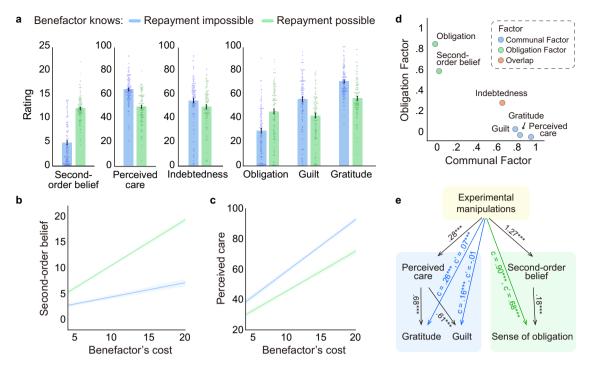


Fig. 4 | **Appraisals and emotional responses to benefactor's help with different intentions. a** Participants' appraisals (i.e., second-order belief of how much the benefactor expected for repayment and perceived care) and emotion ratings (indebtedness, obligation, gratitude, and guilt) in Repayment impossible and Repayment possible conditions. Each dot represents the average rating in the corresponding condition for each participant (*n* = 108 participants). Data are presented as mean values +/– SEM. **b, c** Participant's second-order beliefs of how much the benefactor expected for repayment and perceived care plotted as functions of extra information about benefactor's intention (Repayment impossible vs. Repayment possible) and benefactor's cost. Data are presented as mean values +/– SEM. SEMs were generated via bootstrapping that respected the repeated measurements within each participant (*n* = 24 trials for each condition in Study 2a/28 trials for each condition in Study 2b, 108 participants). **d** Factor analysis showed that participants'

appraisals and emotions could be explained by two independent factors, which appeared to reflect two distinct subjective experiences. The Communal Factor reflects participants' perception that the benefactor cared about their welfare and resulted in emotions of gratitude and guilt (Blue), while the Obligation Factor reflects participants' second-order beliefs about the benefactor's expectation for repayment and the sense of obligation (Green). **e** Simplified schematic representation of mediation analysis. See full model in Fig. S3c. Results showed that second-order beliefs and perceived care appraisals differentially mediated the effects of the experimental manipulations on emotional responses. Second-order beliefs mediated the effects of the experimental manipulations on the sense of obligation (Green), while perceived care mediated the effects of experimental manipulations on gratitude and guilt (Blue).

and emotion ratings in Study 2 revealed that 66% of the variance in ratings could be explained by two factors (Fig. 4d, and Fig. S2e; Fig. S3a, b). The Communal Factor reflected participants' perception that the benefactor cared about their welfare and resulted in emotions of guilt and gratitude, while the Obligation Factor reflected participants' second-order beliefs about the benefactor's expectation for repayment and the sense of obligation. Interestingly, indebtedness moderately loaded on both factors supporting its mixed relationship to guilt and obligation. Second, a mediation analysis revealed that second-order beliefs and perceived care appraisals differentially mediated the effects of the experimental manipulations on emotional responses (total indirect effect = 0.59 ± 0.04 , 95%CI = [0.51, 0.67], Z = 14.49, p < 0.001, two-tailed; model performance: $\chi^2 = 9.68$, df = 4, CFI = 1.00, TLI = 0.997, RMSEA = 0.023, SRMR = 0.004; Fig. 4e and Fig. S3c). Second-order beliefs mediated the effects of the experimental manipulations on obligation (Indirect effect = 0.22 ± 0.03 , 95%CI = [0.16, 0.29], Z = 7.18, p < 0.001), while perceived care mediated the effects of the experimental manipulations on guilt (Indirect effect = 0.17 ± 0.01 , 95%CI = [0.15, 0.20], Z = 13.23, p < 0.001) and gratitude (Indirect effect = 0.19 ± 0.01 , 95%CI = [0.17, 0.22], Z = 13.72, p < 0.001). Together, these results provide further support for the predictions of our conceptual model that indebtedness is comprised of two distinct feelings. The guilt component arises from the belief that the benefactor acts from altruistic intentions (i.e., perceived care), while the obligation component arises when the benefactor's intentions are perceived to be strategic (e.g., expecting repayment).

Beneficiary's behaviors are influenced by benefactor's intentions

Next, we examined participants' behaviors in response to receiving help from a benefactor. Specifically, we were interested in how much participants would reciprocate after receiving the favor and also whether they might outright reject the benefactor's help given the opportunity. We found that participants reciprocated more money as a function of the amount of help received from the benefactor, $\beta = 0.63 \pm 0.02$, 95%CI = [0.59, 0.67], t(109.12) = 25.60, p < 0.001, linear mixed model, two-tailed (Fig. 5a, Table S3). This effect was slightly enhanced in the Repayment impossible condition relative to the Repayment possible condition, $\beta = -0.03 \pm 0.01$, 95%CI = [-0.05, -0.01], t(130.29) = -2.99, p = 0.003. A mixedeffect logistic regression revealed that when given the chance, participants were more likely to reject help in the Repayment possible condition when they reported more obligation (rejection rate = 0.37 ± 0.10), compared to the Repayment impossible condition (rejection rate = 0.30 ± 0.03), $\beta = 0.27 \pm 0.08$, 95%Cl = [0.11, 0.43], z(2788) = 3.64, p < 0.001, two-tailed (Fig. 5b, Table S3). Moreover, as the benefactor's cost increased, participants were less likely to reject the help ($\beta = -0.65 \pm 0.13$, 95%Cl = [-0.90, -0.40], z(2788) = -5.16, p < 0.001). No significant interaction effect

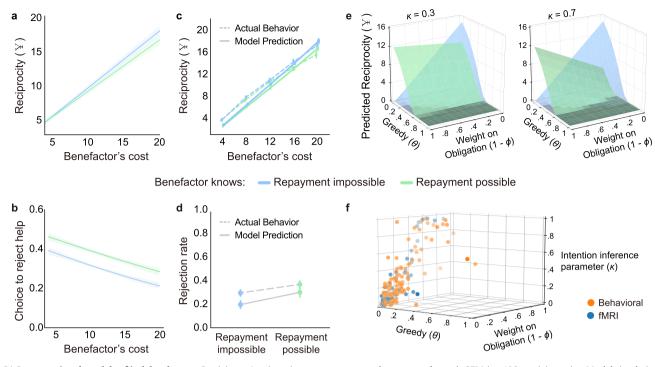


Fig. 5 | **Computational models of indebtedness. a** Participants' reciprocity behavior in each trial plotted as a function of information about benefactor's intention (Repayment impossible vs. Repayment possible) and benefactor's cost. **b** Participants' decisions to accept or reject help in each trial plotted as a logit function of information about benefactor's intention and benefactor's cost. For a and b, data are presented as mean values +/– SEM. SEMs were generated via bootstrapping that respected the repeated measurements within each participant (*n* = 12 trials for each condition in Study 2a/14 trials for each condition in Study 2b, 108 participants). **c** The observed amounts of reciprocity after receiving help and predictions generated by the reciprocity model at each level of the benefactor's cost in Repayment impossible and Repayment possible conditions. **d** The observed rates of rejecting help and predictions generated by the help-acceptance model in Repayment impossible and Repayment possible conditions. For **c** and **d**, data are

between condition and benefactor's cost was observed $(\beta = 0.07 \pm 0.07, 95\%$ CI = [-0.07, 0.21], z(2788) = 1.08, p = 0.279).

Computational models of how indebtedness impacts behavior Building on our conceptual model of indebtedness, we developed two computational models using a Psychological Game Theoretic framework^{34–36} to predict reciprocity and help-acceptance decisions that maximize the beneficiary's expected utility based on the competing latent motivations of self-interest, communal concern (i.e., guilt and gratitude), and obligation (Eq. 1).

$$U(D_B) = \theta_B * \pi_B + (1 - \theta_B) * \left(\phi_B * U_{Communal} + (1 - \phi_B) * U_{Obligation}\right)$$
(1)

The central idea is that upon receiving a favor D_A from a benefactor A, the beneficiary B chooses an action D_B that maximizes his/her overall utility U. This utility is comprised of a mixture of values arising from self-interest π weighted by a greed parameter θ , and feelings of communal concern $U_{Communal}$ and obligation $U_{Obligation}$, which are inferred from the appraisals of D_A and weighted by the parameter ϕ . Larger ϕ values reflect the beneficiary's higher sensitivity to feelings of communal concern relative to obligation. $U_{Communal}$ reflects a linear combination of guilt and gratitude components (see Methods).

The *reciprocity model* (Model 1.1) predicts the amount of money reciprocated to the benefactor, while the *help-acceptance model*

presented as mean values +/- SEM (n = 108 participants). **e** Model simulations for predicted reciprocity behavior in Repayment impossible and Repayment possible conditions at different parameterizations. The *y*-axis shows the average values of the predicted amount of reciprocity across all levels of benefactor's cost. The model predicted reciprocity changes as a function of the tradeoff between communal and obligation feelings based on ϕ and interacts with the intention inference parameter κ . Increased emphasis on obligation corresponds to increased reciprocity to favors in the Repayment possible condition, but decreased reciprocity in the Repayment impossible condition; this effect is amplified as κ increases. **f** Best fitting parameter estimates of the computational model for reciprocity decisions for each participant (n = 108 and n = 53 participants for behavioral and fMRI studies, respectively).

(Model 2.1) predicts binary decisions to accept or reject help. Though the two models are conceptually similar, the values of $U_{Communal}$ and $U_{Obligation}$ are computed slightly differently due to differences in the types of data (i.e., continuous vs. binary decisions) and how appraisals are inferred. It is important to note that in the reciprocity model, we are unable to distinguish between the separate motivations of guilt and gratitude because both positively contribute to reciprocity. In contrast, based on the findings from Study 1, we divide up the parameter space for the help-acceptance model such that $\phi > 0$ indicates a preference for gratitude and motives accepting the help, while $\phi < 0$ indicates a preference for guilt and motives rejecting the help (see Methods).

For both models, we define $U_{Obligation}$ as the appraisal of the amount of money that *B* believes *A* expects them to return (i.e., *B*'s second-order belief E_B ") normalized by *B*'s endowment size γ_B .

$$U_{Obligation} = \begin{cases} -\left(\frac{E_B^{''} - D_B}{\gamma_B}\right)^2 & \text{Reciprocity model} \\ -\frac{E_B^{''}}{\gamma_B} & \text{Help} - \text{acceptance model} \end{cases}$$
(2)

where $E_{B''}$ is operationalized as D_A in the Repayment possible condition and zero in the Repayment impossible condition.

$$E_B'' = \begin{cases} 0 & \text{Repayment impossible condition} \\ D_A & \text{Repayment possible condition} \end{cases}$$
(3)

In contrast, we define $U_{Communal}$ in terms of the appraisal of how much *B* believes *A* cares about their welfare (i.e., perceived care ω_B).

$$U_{Communal} = \begin{cases} -\left(\frac{\omega_B * \gamma_B - D_B}{\gamma_B}\right)^2 & \text{Reciprocity model} \\ \omega_B & \text{Help} - \text{acceptance model} \end{cases}$$
(4)

We assume that *B* infers perceived care ω_B proportional to how much *A* spent D_A from their endowment γ_A and that this effect might be mitigated by the amount of money *B* believes *A* expects them to return (i.e., second-order belief E_B ").

$$\omega_B = \frac{D_A - \kappa_B * E_B''}{\gamma_A} \tag{5}$$

where κ reflects the degree to which the perceived strategic intention E_B'' reduces the perceived altruistic intention ω_B . See details for the models in Methods.

The reciprocity model

We performed a rigorous validation of our reciprocity model (Model 1.1) across a variety of different types of evaluations. First, we were interested in how well our computational model for reciprocity captured trial-to-trial reciprocity decisions. Model parameters were estimated by minimizing the sum of squared error between the model predicted behaviors and participants' reciprocity decisions separately for each participant. Our computational model was able to successfully predict participants' continuous reciprocity decisions after receiving help $(r^2 = 0.79, \beta = 0.88 \pm 0.01, 95\%$ Cl = [0.85, 0.91], t(87.82) = 59.36, p < 0.001, linear mixed model, two-tailed; Fig. 5c; Fig. S6a-c; Table S16) and significantly outperformed other plausible models, such as: (a) a model with linear formulations of utilities for self-interest, communal concern, and obligation (Model 1.2), (b) models that solely included the term for communal concern (Model 1.3) or obligation (Model 1.4) besides the self-interest term. (c) models with separate parameters for self-interest, communal concern, and obligation (Model 1.5 and Model 1.6), (d) a model that assumes participants reciprocate purely based on the benefactors helping behavior (i.e., tit-for-tat) (Model 1.7)^{37,38}, and (e) a model that assumes that participants are motivated to minimize inequity in payments (Model 1.8)^{52,55} (Tables S10 and S11). Parameter recovery tests indicated that the parameters of the reciprocity model were highly identifiable (Pearson correlation between true and recovered parameters over the three parameters, two-tailed, reciprocity $r = 0.94 \pm 0.07$, 95%CI = [0.80, 1.08], t(322) = 50.70, p < 0.001; Table S14).

A simulation of the reciprocity model across varying combinations of the θ , ϕ and κ parameters revealed diverging predictions of the beneficiaries' response to favors in Repayment impossible and Repayment possible conditions (Fig. 5e). Not surprisingly, greedier individuals (higher θ) are less likely to reciprocate others' favors. However, reciprocity changes as a function of the tradeoff between communal and obligation feelings based on ϕ and interacts with the intention inference parameter κ . Increased emphasis on obligation corresponds to increased reciprocity to favors in the Repayment possible condition, but decreased reciprocity in the Repayment impossible condition; this effect is amplified as κ increases. We found that most participants had low θ values (i.e., greed), but showed a wide range of individual differences in κ and ϕ parameters (Fig. 5f). Interestingly, the degree to which the perceived strategic intention reduced the perceived altruistic intention during intention inference κ , was positively associated with the relative weight on obligation $(1 \cdot \phi)$ during reciprocity ($r = 0.79 \pm 0.05$, 95%Cl = [0.70, 0.85], t(106) = 13.14, p < 0.001, Pearson correlation, two-tailed). This suggests that the participants who cared more about the benefactor's strategic intentions also tended to be motivated by obligation when deciding how much money to reciprocate.

Beyond just simply predicting behaviors, we conducted additional validations to assess how well our reciprocity model's predictions of second-order beliefs (E_B "; Eq. 3) and perceived care (ω_B ; Eq. 5) were able to capture trial-to-trial variations in participants' selfreported ratings of appraisals and feelings. Regression analyses showed that the reciprocity model's representations of E_B " and ω_B were associated with trial-to-trial variations in self-reported values of second-order beliefs of the benefactor's expectation for repayment $(\beta = 0.68 \pm 0.03, 95\%$ CI = [0.62, 0.74], t(106.93) = 21.48, p < 0.001, linear mixed model, two-tailed; Fig. S5a, b) and perceived care $(\beta = 0.72 \pm 0.03, 95\%$ CI = [0.66, 0.77], t(107.30) = 26.76, p < 0.001;Fig. S5c, d), respectively. Moreover, *k* appeared to successfully capture individual differences as participants who reported an overall higher level of perceived care were also observed to have a higher overall level of ω_B (r = 0.27 ± 0.09, 95%Cl = [0.09, 0.44], t(106) = 2.92, p = 0.004, Pearson correlation, two-tailed).

We further assessed if the reciprocity model's representations of perceived care (ω_B) and second-order belief (E_B ") appraisals corresponded to self-reported communal and obligation feelings. Supporting our predictions, the reciprocity model's predictions of ω_B significantly predicted self-reported guilt ratings ($\beta = 0.47 \pm 0.03$, 95% CI = [0.42, 0.53], t(105.5) = 17.21, p < 0.001, linear mixed model, two-tailed) as well as the Communal Factor scores obtained from EFA in Fig. 4d ($\beta = 0.81 \pm 0.03$, 95%CI = [0.75, 0.87], t(107.58) = 25.81, p < 0.001), while the model predictions of E_B " significantly predicted self-reported obligation ratings ($\beta = 0.38 \pm 0.03$, 95%CI = [0.32, 0.44], t(106.20) = 12.67, p < 0.001) and the Obligation Factor scores ($\beta = 0.64 \pm 0.06$, 95%CI = [0.56, 0.71], t(106.03) = 15.97, p < 0.001).

The help-acceptance model

Next, we evaluated how well the help-acceptance model (Model 2.1) was able to capture participants' trial-to-trial decisions of whether or not to accept the benefactor's help. We estimated the parameters by maximizing the log-likelihood of the predicted probability of the chosen option (accept or reject) separately for each participant. Overall, we found that our model was able to predict participants' decisions to accept or reject help (accuracy = 80.37%; Fig. 5d; Fig. S6d-f; Table S17). The help-acceptance model outperformed models with separate parameters for self-interest, communal concern, and obligation (Model 2.4 and 2.5), but did not significantly outperform models that solely included terms for communal concern (Model 2.2) or obligation (Model 2.3) (Tables S12 and S13). This likely stems from a slight instability in the parameterization of the model (see Methods and Discussion), which is confirmed by the moderate level of identifiability indicated by the parameter recovery tests (Pearson correlation between true and recovered parameters over the four parameters, two-tailed, $r = 0.43 \pm 0.40$, 95%CI = [-0.35, 1.21], *t*(430) = 9.92, *p* < 0.001; and Table S15).

Communal concern and obligation involve distinct neural processes

Next, in Study 3 (n = 53), we explored the neural bases of indebtedness and examined whether the processing of communal concern and obligation involve differential brain processes as suggested by our conceptual model. Participants completed the same task as Study 2 while undergoing fMRI scanning, except that they were unable to reject help. First, we successfully replicated all of the behavioral results observed in Study 2 (see detailed statistics in Tables S1 and S7, and Figs. S7 and S8). In addition, we found that the two-factor EFA model we estimated using the self-report data in Study 2 generalized well to the independent sample in Study 3 using confirmatory factor analysis (CFA; Fig. S7g), with comparative fit indices exceeding the >0.9 acceptable threshold (CFI=0.986, TLI=0.970) and the root mean

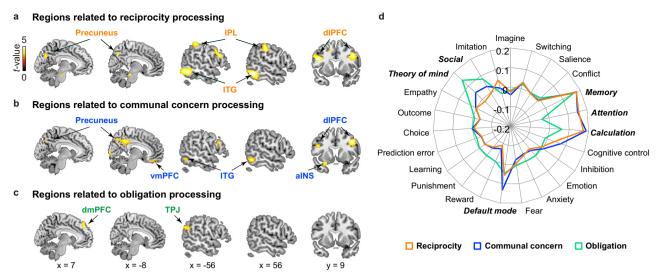


Fig. 6 | **Neural processes associated with reciprocity, communal concern and obligation. a** Brain regions responding to trial-by-trial levels of reciprocity. **b** Brain regions responding parametrically to trial-by-trial communal concern, which depended on the perceived care from the help (ω_B). **c** Brain regions identified in the parametric contrast for obligation (E_B "), the responses of which monotonically increased in the Repayment possible condition relative to the Repayment impossible condition. For **a**-**c**, n = 53 participants. The brain maps were thresholded using

cluster correction FWE p < 0.05 with a cluster-forming threshold of $p < 0.001^{121}$. **d** Results of meta-analytical decoding for the neural correlates of reciprocity, communal concern and obligation, respectively. IPL inferior parietal lobule, dIPFC dorsolateral prefrontal cortex, ITG inferior temporal gyrus, vmPFC ventromedial prefrontal cortex, aINS anterior insula, dmPFC dorsomedial prefrontal lobe, TPJ temporal parietal junction.

square error of approximation and the standardized root mean squared residual were within the reasonable fit range of <0.08 (RMSEA = 0.079, SRMR = 0.019)⁵⁶⁻⁵⁸.

Second, we performed univariate analyses to identify brain processes during the Outcome period (Fig. 3b), where participants learned about the benefactor's decision to help. Using a model-based fMRI analytic approach⁵⁹, we fit three separate general linear models (GLMs) to each voxel's timeseries to identify brain regions that tracked different components of the computational model. These included trialby-trial values for: (1) the amount of reciprocity, (2) communal concern, which depended on the perceived care from the help (ω_B), and (3) obligation, which depended on the second-order belief of the benefactor's expectation for repayment (E_B'') (see Methods). We found that trial-by-trial reciprocity behavior correlated with activity in bilateral dIPFC, bilateral inferior parietal lobule (IPL), precuneus, and bilateral inferior temporal gyrus (ITG) (Fig. 6a, Table S18). Trial-by-trial communal feelings tracked with activity in the anterior insula, vmPFC, precuneus, bilateral dlPFC, and bilateral ITG (Fig. 6b; Table S18). The processing of obligation was associated with activations in dmPFC and left TPJ (Fig. 6c, Table S18).

To aid in interpreting these results, we performed meta-analytic decoding⁶⁰ using the Neurosynth database⁶¹. Reciprocity-related activity was primarily associated with "Attention," "Calculation," and "Memory" terms. Communal feelings related activity was similar to the reciprocity results, but was additionally associated with "Default mode" term. Obligation activity was highly associated with terms related to "Social," "Theory of mind (ToM)," and "Memory" (Fig. 6d). Together, these neuroimaging results reveal differential neural correlates of feelings of communal concern and obligation and support the role of intention inference in the generation of these feelings proposed by our conceptual model. The processing of communal feelings was associated with activity in vmPFC, an area in default mode network that has been linked to gratitude⁶²⁻⁶⁴, positive social value, and kind intention^{65,66}, as well as the insula, which has been previously related to guilt^{54,67,68}. In contrast, the processing of obligation was associated with activations of theory of mind network, including dmPFC and TPJ, which is commonly observed when representing other peoples' intentions or strategies^{66,69,70}.

Neural utility model of indebtedness predicts reciprocity behavior

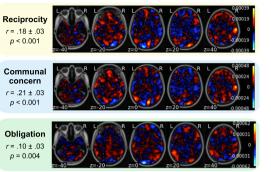
Finally, we sought to test whether we could use signals directly from the brain to construct a utility function and predict reciprocity decisions (Fig. 7a). Using brain activity during the Outcome period of the task (Fig. 3b), we trained two whole-brain models using principal components regression with 5-fold crossvalidation⁷¹⁻⁷³ to predict the appraisals associated with communal concern (ω_B) and obligation (E_B ") separately for each participant. These whole-brain patterns were able to successfully predict the model representations of these feelings for each participant on new trials, though with modest effect sizes (communal concern pattern: average $r = 0.21 \pm 0.03$, 95%CI = [0.15, 0.27], t(52) = 7.00,*p_{nerm}* < 0.001, one-sample permutation *t*-test, two-tailed; obligation pattern: average $r = 0.10 \pm 0.03$, 95%CI = [0.04, 0.16], t(52) = 3.33, $p_{perm} = 0.004$; Fig. 7a). Moreover, these patterns appear to be capturing distinct information as they were not spatially correlated, $r = 0.03 \pm 0.04$, 95%CI = [-0.05, 0.11], p = 0.585. These results did not simply reflect differences between the Repayment possible and Repayment impossible conditions as the results were still significant after controlling for this experimental manipulation (communal concern: average $r = 0.18 \pm 0.02$, 95%CI = [0.14, 0.22], t(52) = 9.00, $p_{perm} < 0.001$; obligation: average $r = 0.04 \pm 0.02$, 95% $CI = [-0.02, 0.08], t(52) = 2.00, p_{perm} = 0.024).$ Furthermore, we were unable to successfully discriminate between these two conditions using a whole brain classifier (accuracy = $55.0 \pm 1.25\%$, permutation p = 0.746).

Next, we assessed the degree to which our brain models could account for reciprocity behavior. We used cross-validated neural predictions of communal concern (ω_B) and obligation (E_B ") feelings as inputs to our computational model of reciprocity behavior instead of the original terms:

$$U(D_{B}) = \theta_{B} * \pi_{B} + (1 - \theta_{B}) \\ * \left(\phi_{B} * \overrightarrow{\beta_{map}} \cdot \overrightarrow{Commual_{map}} + (1 - \phi_{B}) * \overrightarrow{\beta_{map}} \cdot \overrightarrow{Obligation_{map}} \right)$$

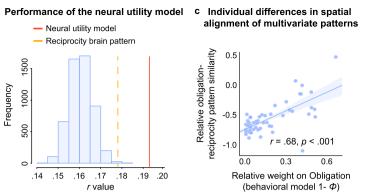
$$(6)$$





b

Fig. 7 | **Neural utility model of indebtedness. a** Unthresholded multivariate patterns used to predict the amounts of reciprocity (Yellow), trial-by-trial communal concern (ω_B , Blue) and obligation (E_B ", Green) separately. **b** We assessed the importance of the participant-specific model parameters estimated from the neural utility model (i.e., ϕ) by generating a null distribution of predictions after permuting the estimated ϕ parameter across participants 5,000 times. The red line indicates the performance of our neural utility model (*r* value of prediction), and the orange line indicates the performance of the whole-brain model trained to directly predict reciprocity. The subject-specific weightings were important in



predicting behavior as our neural utility model significantly outperformed a null distribution of average prediction accuracy after randomly shuffling the participant weights (Blue). **c** The relationship between the relative weight on obligation $(1 - \phi)$ derived from behavior and a neurally derived metric of how much obligation vs. communal feelings influenced reciprocity behavior (Pearson correlation, two-tailed, $r = 0.68 \pm 0.09$, 95%CI = [0.51, 0.81], t(51) = 6.69, p < 0.001, n = 53 participants). Data are presented as regression line +/- 95% confidence interval for the regression.

where $\overrightarrow{\beta_{map}}$ refers to the pattern of brain activity during the Outcome

period (Fig. 3b) of a single trial and $\overrightarrow{Commual}_{map}$ and $\overrightarrow{Obligation}_{map}$ refer to the multivariate brain models predictive of each participant's communal concern and obligation utilities respectively. We were able to reliably predict reciprocity behavior with our computational model informed only by predictions of communal and obligation feelings derived purely from brain responses (average $r = 0.19 \pm 0.02$, 95%CI = [0.15, 0.23], t(52) = 9.50, $p_{perm} < 0.001$; AIC = 317.70 ± 5.00; Fig. 7b). As a benchmark, this model numerically outperformed a whole-brain model trained to directly predict reciprocity (average $r = 0.18 \pm 0.03$, 95%CI = [0.12, 0.24], t(52) = 6.00, $p_{perm} < 0.001$; AIC = 317.54 ± 5.00; Fig. 7a), but this difference did not reach statistical significance (t(52) = 1.64, p = 0.108, Cohen's d = 0.23, 95%CI = [-0.002, 0.022], permutation-based paired t-test, two-tailed).

We performed several additional validations of the neural utility model to demonstrate its overall performance. First, we found that the parameter ϕ estimated from the neural utility model, which reflects the tradeoff between communal concern and obligation, strongly correlated with the same parameter estimated from the behavioral computational model across participants ($r = 0.88 \pm 0.04$, 95%Cl = [0.80, 0.93], t(51) = 13.3, p < 0.001, Pearson correlation, two-tailed). Second, we assessed the individual specificity of ϕ derived from the neural utility model, to test how uniquely sensitive individuals are to communal concern versus obligation. To do so, we generated a null distribution of predictions after permuting the estimated ϕ parameter across participants 5,000 times. We found that the participant-specific weightings were highly important in predicting behavior as our neural utility model significantly outperformed null models using randomly shuffled ϕ parameters, $p_{perm} < 0.001$ (Fig. 7b). Third, we tested how well our neural-utility model reflected the trade-off between an individual's feelings of communal concern and obligation estimated from the behavioral model. We hypothesized that the relative influence of a particular feeling on behavior should be reflected in the spatial alignment of their corresponding brain patterns⁷⁴ (see Methods). Our results support this hypothesis. Participants who cared more about obligation relative to communal concern (higher behavioral $1 - \phi$) also exhibited greater spatial alignment between their obligation and reciprocity brain patterns relative to communal concern and reciprocity patterns (Fig. 7c; $r = 0.68 \pm 0.09$, 95%CI = [0.51, 0.81], t(51) = 6.69,

p < 0.001, Pearson correlation, two-tailed). These results provide evidence at the neural level indicating that individuals appear to trade-off between feelings of communal concern and obligation when deciding how much to reciprocate after receiving help from a benefactor.

Discussion

Gift-giving, favor-exchanges, and providing assistance are behavioral expressions of relationships between individuals or groups. While favors from friends and family often engender reciprocity and gratitude, they can also elicit guilt in a beneficiary who may feel that they have burdened a benefactor. Favors in more transactive relationships, however, can evoke a sense of obligation in the beneficiary to repay the favor. In this study, we sought to develop a conceptual model of indebtedness that outlines how appraisals about the intentions behind a favor are critical to the generation of these distinct feelings, which in turn motivates how willing individuals are to accept or reject help and ultimately reciprocate the favor.

We provide a systematic validation of this conceptual model of indebtedness across three separate experiments by combining a largescale online questionnaire, behavioral measurements in an interpersonal game, computational modeling, and neuroimaging. First, we used an open-ended survey to capture lay intuitions about indebtedness based on regression analysis of past emotional experiences and topic modeling based-text analysis of self-reported definitions. Overall, we find strong support that the feeling of indebtedness can be further separated into two distinct components-guilt for burdening the favor-doer and obligation to repay the favor. Using topic modeling on lay definitions of indebtedness, we find that guilt and gratitude appear to load on the same topic, while feeling words pertaining to burden and negative body states load on a separate topic. Second, we used a laboratory task designed to elicit indebtedness in the context of an interpersonal interaction and specifically manipulated information intended to shift the benefactor's perceptions of the beneficiary's intentions underlying their decisions. Although our manipulation was subtle, we find that it was able to successfully change participants' appraisals about how much the beneficiary cared about them and their beliefs about how much money the benefactor expected in return. Consistent with appraisal theory²⁸⁻³³, these shifts in appraisals influenced participants' subjective feelings and ultimately their behaviors. Intentions perceived to be altruistic led to increased guilt and gratitude, while intentions viewed as more strategic increased feelings of

obligation. While all three feelings increased reciprocity decisions, the guilt and obligation components of indebtedness increased the probability of rejecting help when that option was available to the participant.

One contribution of this work is the use of computational modeling to predict reciprocity and help-acceptance decisions in our interpersonal task based on our conceptual model of indebtedness. The majority of empirical research on indebtedness^{21,46,47,75} and other emotions^{76,77} has relied on participants' self-reported feelings in response to explicit questions regarding social emotions, which has significant limitations, such as its dependence on participants' ability to introspect^{78,79}. Formalizing emotions using computational models is critical to advancing theory, characterizing their impact on behavior, and identifying associated neural and physiological substrates^{39,80,81}. However, the application of computational modeling to the study of social emotions is a relatively new enterprise^{39,54,82,83}. Previous research has had success modeling belief-dependent utility using Psychological Game Theory^{36,37} in interactive social contexts. Building on this work, we model participants' appraisals and emotions²⁸⁻³³ based on the state of the game to predict two different types of decisions (i.e., reciprocity & help-acceptance)³⁹. The current work contributes to a growing family of game theoretic models of social emotions such as guilt^{34,54}, gratitude⁸⁴, and anger^{85,86}, and can be used to infer feelings in the absence of self-report, providing avenues for investigating other social emotions.

We provide a rigorous validation of our computational models using behaviors in the interpersonal game, self-reported subjective experiences, and neuroimaging. First, we can accurately predict participants' reciprocity and help-acceptance decisions. Second, we observed that the model predictions of second-order belief and perceived care in the reciprocity model accurately captured participant's trial-to-trial self-reported appraisal and feeling ratings. Third, our brain imaging analyses demonstrate that each feeling reflects a distinct psychological process, and that intention inference plays a key role during this process. Consistent with previous work on guilt^{54,67,68,87} and gratitude⁶²⁻⁶⁴, our model representation of communal concern correlated with increased activity in the insula, dIPFC, and default mode network including the vmPFC and precuneus. Obligation, in contrast, captured participants' second order beliefs about expectations of repayment and correlated with increased activation in regions routinely observed in mentalizing including the dmPFC and TPJ^{66,69,70}.

We provide an even stronger test of our ability to characterize the neural processes associated with indebtedness by deriving a "neural utility" model. Previous work has demonstrated that it is possible to build brain models of preferences that can predict behaviors^{88,89} and the hidden motives behind the behaviors⁹⁰. Here, we trained multivoxel patterns of brain activity to predict participants' communal and obligation utility. We then used these brainderived representations of communal concern and obligation to predict how much money participants ultimately reciprocated to the beneficiary. Remarkably, we found that this neural utility model of indebtedness was able to predict individual decisions entirely from brain activity and numerically outperformed (but not significantly) a control model that provided a theoretical upper bound of how well reciprocity behavior can be predicted directly from brain activity. Importantly, the neural utility model was able to accurately capture each participant's preference for communal concern relative to obligation. We observed a significant drop in our ability to predict behavior when we randomly shuffled the weighting parameter across participants. In addition, we find that the more the pattern of brain activity predicting reciprocity behavior resembled brain patterns predictive of communal concern or obligation, the more our behavioral computational model weighted this feeling in predicting behavior, demonstrating that these distinct appraisals/feelings are involved in motivating reciprocity decisions.

This work advances our theoretical understanding of social emotions. First, we highlight the complex relationship between gratitude and indebtedness. We propose that feeling cared for by a benefactor, which we call communal concern^{44,45}, is comprised of both guilt and gratitude. Each emotion diverges in valence, with gratitude being positive⁶⁻⁹, and guilt being negative^{40-42,44,54}, but both promote reciprocity behavior. When faced with the offer of help, anticipated gratitude should motivate the beneficiary to accept help in order to establish or promote a relationship^{6,7}, whereas anticipated guilt should motivate the beneficiary to reject help out of concern to protect the benefactor from incurring a cost^{44,54,91}. Although we observed support for this prediction, our interpersonal task was not designed to explicitly differentiate guilt from gratitude, which limited the ability of our reciprocity model to capture the specific contributions of guilt and gratitude to communal concern and likely impacted identifiability of the parameters of the help-acceptance model. Future work might continue to refine the relationship between these two aspects of communal concern both in terms of behaviors in experiments and computations in models^{54,62-64,67,68,87}.

Second, our conceptual model provides a framework to better understand the role of relationships and contexts in generating feelings of indebtedness within a single individual. Different types of relationships (see Clark and Mills's theory of communal and exchange relationships^{4,5}, and Alan Fiske's Relational Models Theory⁹²) have been theorized to emphasize different goals and social norms which can impact social emotions⁹³⁻⁹⁵. For example, communal relationships prioritize the greater good of the community and are more conducive to altruistic sharing, which can be signaled by altruistic favors³⁻⁵. In contrast, exchange relationships are more transactional in nature^{2,4,5,10-12} and emphasize maintaining equity in the relationship, which can be signaled by strategic favors⁹². Our conceptual model proposes that perceptions of the benefactor's intentions directly impact the feelings experienced by the beneficiary (e.g., guilt & obligation). Although we deliberately attempted to minimize aspects of the relationship between the benefactor and beneficiary by making players anonymous to control for reputational effects. future work might experimentally manipulate these relationships to directly test the hypothesis that relationship types differentially moderate the responses of gratitude and subcomponents of indebtedness.

Third, we present evidence exploring the relationship between indebtedness and guilt. Guilt and indebtedness are interesting emotions in that they are both negatively valenced, yet promote prosocial behaviors. In previous work, we have operationalized guilt as arising from disappointing a relationship partner's expectations^{39,54,55,96}, which is conceptually related to the feeling of obligation in this paper. This feeling results from disappointing a relationship partner or violating a norm of reciprocity and is a motivational sentiment evoked by social expectations reflecting a "sense of should" that is associated with other negative affective responses such as feelings of pressure, burden, anxiety, and even resentment⁴⁹⁻⁵¹. In other work, we have investigated how guilt can arise from causing unintended harm to a relationship partner^{68,97}. This is conceptually more similar to how we frame guilt here, which arises from the feeling that one has unnecessarily burdened a relationship partner even though the help was never explicitly requested by the beneficiary. We believe that continuing efforts to refine mathematical models of emotions across a range of contexts, will eventually allow the field to move beyond relying on the restrictive and imprecise semantics of linguistic labels to define emotion categories (e.g., guilt, gratitude, indebtedness, obligation, feeling, motivation, etc.).

Our study has several potential limitations, which are important to acknowledge. First, although we directly and conceptually replicate our key findings across multiple samples, all of our experiments recruit experimental samples from a Chinese population. It is possible that there are cultural differences in the experience of indebtedness, which may not generalize to other parts of the world. For example, compared with Westerners who commonly express gratitude when receiving benevolent help. Japanese participants (East Asian population) often respond with "Thank you" or "I am sorry", indicating their higher experience of guilt after receiving favors^{40,41}. Cultural differences may perhaps reflect how the two components of indebtedness are weighted, with guilt being potentially more prominent in East Asian compared to Western populations, reflecting broader cultural differences in collectivism and individualism. Second, our computational models may oversimplify the appraisal and emotion generating processes. These models operationalize the appraisals of perceived care and second-order belief using information available to each participant in the task (i.e., benefactor's helping behavior and manipulation about the participant's ability to reciprocate), which may not generalize to other experimental contexts without modification. Although our computational models performed well in capturing participants' behaviors in this task, we emphasize the importance of continued refinement. Third, future research is needed to extend our conceptual model by differentiating different types of help-receiving events (e.g., help when moving to a new apartment vs. help during a period of sickness) and manipulating other related contexts, such as giftreceiving²³ and help-seeking¹⁷.

In summary, in this study, we develop a comprehensive and systematic conceptual model of indebtedness and validate it across three studies combining a large-scale online questionnaire, an interpersonal game, computational modeling and neuroimaging. A key aspect to this work is the emphasis on the role of appraisals about the intentions behind a favor in generating distinct feelings of guilt and obligation, which in turn motivates how willing beneficiaries are to accept or reject help and ultimately reciprocate the favor. Together, these findings highlight the psychological, computational, and neural mechanisms underlying the hidden costs of receiving favors^{22–24}.

Methods

Participants

For Study 1, participants (1808 graduate and undergraduate students) were recruited from Zhengzhou University, China to complete an online questionnaire. Participants were excluded if they filled in information irrelevant to the question or experiment in the essay question (e.g., this question is boring, or I don't want to answer this question; 189 participants), leaving 1619 participants (self-reported gender: 812 females, 18.9 ± 2.0 (SD) years). While 98.7% of participants reported the events of receiving help, 24.4% of participants reported the events of rejecting help within the past 1 year, resulting in 1991 effective daily events (1598 help-acceptance events and 395 helprejection events). To extract the words related to emotions and feelings in the definition of indebtedness, 80 additional graduate and undergraduate students (45 females, 22.6 ± 2.58 years) were recruited from different universities in Beijing to complete an online word classification task (see Supplementary Methods). No data were excluded from the analysis in the task.

For Study 2a (behavioral study), 58 graduate and undergraduate Chinese Han students were recruited from Zhengzhou University, China, and 7 participants were excluded due to equipment malfunction, leaving 51 participants (self-reported gender: 33 females, 19.9 ± 1.6 years) for data analysis. For Study 2b (behavioral study), 60 graduate and undergraduate Chinese Han students were recruited from Zhengzhou University, China, and 3 participants were excluded due to failing to respond in more than 10 trials, leaving 57 participants (45 females, 20.1 ± 1.8 years) for data analyses.

For Study 3, 57 right-handed healthy graduate and undergraduate Chinese Han students from Beijing, China took part in the fMRI scanning. Four participants with excessive head movements (>2 mm) were excluded, leaving 53 participants (self-reported gender: 29 females, 20.9 \pm 2.3 years) for data analysis. For all experiments, none of the participants reported any history of psychiatric, neurological, or cognitive disorders. No statistical method was used to predetermine sample size. All experiments were carried out in accordance with the Declaration of Helsinki and were approved by the Ethics Committee of the School of Psychological and Cognitive Sciences, Peking University. Informed written consent was obtained from each participant prior to participating.

Experimental procedures

Study 1-Online questionnaire. All participants completed the same questionnaire on the Questionnaire Star platform (https://www.wix. cn/) online using their mobile phones. The questionnaire consisted of two parts. Each participant was asked to recall a daily event in which they received help (part 1) or rejected help (part 2) from others, and to answer the questions regarding their appraisals (second-order belief and perceived care), emotions (gratitude, indebtedness, guilt, and obligation), behaviors (the need to reciprocate and whether to reject help) and other details of this event (e.g., the relationship with the benefactor, the participant's benefit, and the benefactor's cost). To explore how participants defined indebtedness, we asked participants to answer the following two questions about the definition of indebtedness after recalling the event: (1) In the context of helping and receiving help, what is your definition of indebtedness? (Fill-in-theblanks test) (2) In daily life, what do you think is/are the source(s) of indebtedness? Multiple-choice question with four options "Negative feeling for harming the benefactor", "Negative feeling for the pressure to repay caused by other's ulterior intentions", "Both" and "Neither". See the online questionnaire in Supplementary Methods.

Study 2-Interpersonal task. During Session 1 (the main task), each participant played multiple single-shot rounds of the interpersonal task (Fig. 3) as a Receiver. In each trial, the participant was paired with an anonymous same-gender Decider (co-player), and was informed that the co-player in each trial was distinct from the ones in any other trials and only interacted with the participant once during the experiment. In each round, the participant had to receive a 20-second pain stimulation with the intensity of 6. The participant was instructed that each co-player: (a) had come to the lab before the participant, (b) had been endowed with 20 yuan (~\$2.7 USD), and (c) had decided whether and how much to spend from this endowment to help the participant reduce the duration of pain (i.e., benefactor's cost, D_A). The more the benefactor spent, the shorter the duration of the participant's pain experience. The maximum pain reduction was 16 s to ensure that participants had some amount of pain on each trial. Unbeknownst to the participant, the benefactor's costs were predetermined by the computer program (Table S2).

Each trial began by informing the participant which Decider from Stage 1 was randomly selected as the co-player for the current trial (Information period, 4 s), with the blurred photo and the participant ID of the co-player, and extra information regarding the co-player's intention to help (see below). The co-player's decision on how much they chose to spend to help the participant was presented (Outcome period, 5 s). Next, the participant indicated how much they thought this co-player expected them to reciprocate (i.e., Second-order belief of the co-player's expectation for repayment; continuous rating scale from 0 to 25 using mouse, step of 0.1 yuan, < 8 s). In half of the trials, the participant had to passively accept the co-player's help (forceaccept situation). The sentence "You have to accept this help" was presented on the screen (4 s). In the other half, the participant could decide whether or not to accept the co-player's help (free-choice situation, < 4 s). The order of options was counterbalanced across trials. If the participant accepted the help, the co-player's cost and the participant's pain reduction in this trial would be realized according to the co-player's decision; if the participant did not accept the help, the co-player would spend no money and the duration of participant's pain stimulation would be the full 20 s. At the end of each trial, the participant was endowed with 25 yuan (-3.4 USD) and decided how much they wanted to allocate to the co-player as reciprocity in this trial from this endowment (D_B , continuous choice from 0 to 25 using mouse, step of 0.1 yuan, < 8 s). We focused on two types of behaviors in this help-receiving context: (1) the participant's amounts of allocation when they passively accept the co-player's help (i.e., reciprocity decisions), and (2) the participant's decisions of whether to accept or reject help in free-choice situation (i.e., help-acceptance decisions).

We manipulated the perceived intention of the co-player (i.e., the benefactor) by providing participants with extra information regarding the co-player's expectation of reciprocity (i.e., extra information about benefactor's intention) below the co-player's subject id at the beginning of each trial. Each participant was instructed that before making decisions, some co-players were informed that the participant would be endowed with 25 yuan and could decide whether to allocate some endowments to them as reciprocity (i.e., Repayment possible condition). The other co-players were informed that the participant had no chance to reciprocate after receiving help (i.e., Repayment impossible condition). In fact, participants could reciprocate in both conditions during the task. The endowment of the co-player (γ_A) was always 20 yuan, and the endowment of the participant (y_B) in each trial was always 25 yuan. The endowment of the participant was always larger than the endowment of the co-player to make the participant believe that the co-player expected repayments in Repayment possible condition.

In Study 2a, we manipulated the participant's beliefs about the benefactor's intentions (condition: Repayment possible vs. Repayment impossible) and the benefactor's cost in a within-subject design. In Study 2b, to disentangle the effect of the benefactor's cost and participant's benefit (i.e., pain reduction), we additionally manipulated the exchange rate between the co-player's cost and participant's pain reduction (i.e., efficiency; the efficiency was always 1.0 in Study 2a) in a within-subject design.

During Session 2 of the interpersonal task, all of the trials from Session 1 were displayed again in a random order. The participant was asked to recall how much they believed the benefactor cared about them, as well as their feelings of indebtedness, obligation, guilt, and gratitude at the time point when they had received the help of the co-player, but had not indicated decisions of accept/ reject help and the amount of reciprocity. Ratings were conducted on a scale from 0 to 100, with 0 represented "not at all" and 100 represented "extremely intense". At the end of the experiment, five trials in Session 1 were randomly selected to be realized. See Supplementary Methods for additional details about procedures and experimental designs.

Study 3–FMRI study

Each participant came to the scanning room individually. The two sessions of the task in the fMRI study were identical to Study 2a, except that participants always had to accept their co-player's help. Session 1 (the main task; Fig. 3b) was conducted in the fMRI scanner, while Sessions 2 was conducted after participants exited the scanner. Before and after each period, a fixation cross was presented for a variable interval ranging from 2 to 6 s, which was for the purpose of fMRI signal deconvolution. See Supplementary Methods for additional details about procedures and experimental designs.

Data analyses in Study 1 (online questionnaire)

Validating conceptual model with emotion ratings. We first attempted to validate the conceptual model using the emotional ratings for daily-life events of receiving and rejecting help obtained from online-questionnaire in Study 1. We conducted between-participant linear regressions predicting indebtedness ratings from guilt and obligation ratings (see Supplementary Methods). Validating conceptual model with self-reported appraisals. Next, we summarized participants' self-reported sources of their feelings of indebtedness. We calculated the frequency that participants selected each of the four options in the question "In daily life, what do you think is/ are the source(s) of indebtedness?" in Study 1 (Fig. S1A), as well as how often that participants attributed "Negative feeling for harming the benefactor" and "Negative feeling for the pressure to repay caused by other's ulterior intentions" as the sources of indebtedness (i.e., the frequency of choosing each single option plus the frequency of choosing "Both of the above").

Validating conceptual model with topic modeling. We also attempted to validate the conceptual model by applying topic modeling to participant's open-ended responses describing their own definition of indebtedness in Study 1. We conducted word-splitting, counted the frequency that each participant used each word and transformed these frequencies using Term Frequency-Inverse Document Frequency (TF-IDF)98,99. The 100 words with the highest weight/ frequency in the definitions of indebtedness were extracted (Table S20). These 100 words were then classified by an independent sample of participants (n = 80) into levels of appraisal, emotion, behavior, person and other. We conducted Latent Dirichlet Allocation (LDA) based topic modeling on the emotional words of indebtedness using collapsed Gibbs sampling. We selected the best number of topics by comparing the models with topic numbers ranging from 2 to 15 using 5-fold cross validation. Model goodness of fit was assessed using perplexity¹⁰⁰. We found that the two-topic solution performed the best (Fig. S1c). See Supplementary Methods for additional details about topic modeling.

Validating conceptual model with self-reported behaviors. We next sought to test the predictions of the conceptual model using the selfreported behaviors from Study 1. First, we used data from Part 1 of the questionnaire (help-receiving events) and used linear regression to predict self-reported need to reciprocate from self-reported feelings of indebtedness, guilt, obligation and gratitude. Second, we combined the data of the events associated with receiving (Part 1) and rejecting help (Part 2) and used logistic regression to classify rejecting from accepting behavior using self-reported counterfactual ratings of indebtedness, guilt, and obligation, and gratitude.

Data analyses in Study 2 (interpersonal task)

The effects of experimental manipulations on participants' appraisal, emotional and behavioral responses. To test the effects of experimental manipulations on beneficiary's appraisals (i.e., second-order belief and perceived care), emotions (i.e., gratitude, indebted-ness, guilt, and obligation) and behaviors (reciprocity and help-acceptance decisions), we conducted linear mixed effects analyses for each dependent variable separately with the benefactor's cost, extra information about benefactor's intention (Repayment possible vs. Repayment impossible) and their interaction effect as fixed effects and the participant ID as a random intercept and slope (see Supplementary Methods).

Relationships between appraisals and emotions. To reveal the relationships between appraisals (i.e., second-order belief and perceived care) and emotions (i.e., indebtedness, guilt, obligation, and gratitude), we estimated the correlations between these variables at both within-participant (Fig. S3a, Table S8) and between-participant levels (Fig. S3b, Table S9). Given the strong correlations between appraisals and emotions (Fig. S3a, b, Tables S8 and S9), we conducted a factor analysis to examine the relationship between appraisals and emotions¹⁰¹. We first applied EFA in Study 2 to identify the number of common factors and the relationships between appraisals and emotions. Next, we conducted CFA using the data of Study 3 to test the two-factor model built by

https://doi.org/10.1038/s41467-023-44286-9

Study 2 in an independent sample. Finally, to test whether the two appraisals mediated the observed effects of experimental variables on emotional responses, we conducted a multivariate mediation analysis using structural equation modeling. See Supplementary Methods for additional details about EFA, CFA, and mediation analysis.

Computational modeling. We built separate computational models predicting participant's reciprocity decisions and help-acceptance decisions based on the conceptual model of indebtedness (see Table S19 for all model object definitions). The utility of each behavior $U(D_B)$ was modeled based on the competing latent motivations of self-interest, communal concern (guilt and gratitude), and obligation using Eq. 1.

For reciprocity decisions, self-interest π_B was defined as the percentage of money kept by the participant out of their endowment γ_B . For help-acceptance decisions, self-interest π_B for accepting help was defined as the percentage of pain reduction from the maximum amount possible, which depended on how much the benefactor spent to help D_A and the exchange rate between the benefactor's cost and the participant's benefit μ (i.e., help efficiency).

$$\pi_{B} = \begin{cases} \frac{\gamma_{B} - D_{B}}{\gamma_{B}} & \text{Reciprocity model} \\ \frac{D_{A} * \mu}{\max(D_{A} * \mu)} & \text{Help} - \text{acceptance model} \end{cases}$$
(7)

For each trial, we modeled the participant's second-order belief $E_B^{"}$ of how much they believed the benefactor expected them to reciprocate (Eq. 3) based on the amount of help offered by the benefactor D_A and whether the benefactor knew repayment was possible. In the Repayment impossible condition, participants knew that the benefactor did not expect them to reciprocate, so we set $E_B^{"}$ to zero. However, in the Repayment possible condition, the benefactor knew that the participant had money that they could spend to repay the favor. In this condition, we modeled the $E_B^{"}$ as proportional to the amount of money the benefactor spent to help the participant.

The appraisals of perceived care ω_B (Eq. 5) were defined as a function of the benefactor's cost D_A and second-order belief E_B ". Specifically, we assumed that the perceived care from help increased as a linear function of how much the benefactor spent D_A from his/her endowment y_A . In other words, the more the benefactor spent, the more care the participant would perceive from the help. However, we assume that this effect is mitigated by the second-order belief of the benefactor's expectation for repayment E_B ". That is, when faced with a specific amount of benefactor's cost, if the participant thought this benefactor expected more repayment, the less care the participant would perceive from the help. Here, the parameter κ ranges from [0, 1] and represents the degree to which the perceived strategic intention $E_{B'}$ reduces the perceived altruistic intention ω_B . This creates a nonlinear relationship between ω_B and E_B'' such that the relationship is negative when k is close to one, positive when k is close to zero, and uncorrelated in the current dataset with $\kappa = 0.32 \pm 0.01$, $\beta = -0.03 \pm 0.03$, 95%Cl = [-0.09, 0.03], t(112.32) = -1.23, p = 0.222 (Fig. S4).

Furthermore, our conceptual model proposed that the feelings of obligation and communal concern (guilt and gratitude) stem from the appraisals of benefactor's strategic intention (i.e., second-order belief) and altruistic intention (i.e., perceived care from the help), respectively. This hypothesis was supported by the results of the mediation analysis (Fig. 4e). Thus, we modeled the utilities of obligation and communal concern (i.e., $U_{Obligation}$ and $U_{Communal}$) as the functions of E_B " and ω_B , respectively (Eqs. 2 and 4).

Predicting reciprocity decisions. To predict continuous reciprocity decisions, we assume that participants were motivated to meet the expectation of the benefactor due to the sense of obligation, and thus maximized $U_{Obligation}$ by minimizing the difference between the

amount they reciprocated D_B and their second-order belief of how much they believed the benefactor expected them to return E_B ", scaled by the participant's endowment size γ_B (Eq. 2). We note that our mathematical operationalization of obligation here is more akin to how we have previously modeled guilt from disappointing others in previous work^{34,39,54,55} (see also Discussion). We also assumed that participants were motivated to reciprocate in response to the benefactor's perceived care due to guilt and gratitude (i.e., communal concern), and thus maximized $U_{Communal}$ by minimizing the difference between the benefactor's reciprocity D_B and their perception of how much they believed the benefactor cared about them ω_B , scaled by the participant's endowment size γ_B (Eq. 4).

Based on our conceptual model (Fig. 1), we defined $U_{Communal}$ as a mixture of feelings of gratitude $U_{Gratitude}$ and guilt U_{Guilt} , in which the parameter δ_B ranged from [0,1] and reflected how much gratitude contributed to communal concern in comparison to guilt.

$$U_{Communal} = \delta_B * U_{Gratitude} + (1 - \delta_B) * U_{Guilt}$$
(8)

We note that both guilt and gratitude positively contribute to reciprocity and our interpersonal task was not designed to explicitly differentiate the effects of guilt and gratitude, which precluded our ability to estimate the specific value of δ_B for predicting reciprocity decisions due to a lack of identifiability. Thus, in this paper we can only make inferences about the broader $U_{Communal}$, which may reflect guilt and/or gratitude. However, our help-acceptance model does attempt to differentiate the contributions of guilt and gratitude to decisions of whether or not to accept help as discussed below.

We modeled the utility U associated with the participants' reciprocity decisions D_B after receiving help in Eq. 1, where ϕ is a free parameter constrained between [0, 1] that captures the trade-off between feelings of communal concern and obligation. The reciprocity model (Model 1.1, Eq. 9) selects the participant's decision D_B associated with the highest utility.

$$U(D_B) = \theta_B * \frac{\gamma_B - D_B}{\gamma_B} - (1 - \theta_B) \\ * \left(\phi_B * \left(\frac{\omega_B * \gamma_B - D_B}{\gamma_B} \right)^2 + (1 - \phi_B) * \left(\frac{E_B'' - D_B}{\gamma_B} \right)^2 \right)$$
(9)

Predicting help-acceptance decisions. We created a separate model (Model 2.1, Eq. 10) to predict help-acceptance decisions. $U_{Obligation}$ was defined as a linear function of E_B'' (Eq. 2). $U_{Communal}$ was defined as a linear function of ω_B (Eq. 4). We modeled the utility of accepting and rejecting help as:

$$\begin{cases} U(Accept) = \theta_B * \pi_B + (1 - \theta_B) * (\phi_B * U_{Communal} - (1 - |\phi_B|) * U_{Obligation}) \\ = \theta_B * \frac{D_A * \mu}{\max(D_A * \mu)} + (1 - \theta_B) * (\phi_B * \omega_B - (1 - |\phi_B|) * \frac{F_B'}{\gamma_B}) \\ U(Reject) = 0 \end{cases}$$
(10)

In this model, *U*(*Reject*) was set to zero, because the participant's emotional responses would not change if the participant did not accept help. Increased obligation reduces the likelihood of accepting help to avoid being in the benefactor's debt^{13,14,102}. In contrast, *U*_{Communal} has a more nuanced influence on behavior, with guilt decreasing the likelihood of accepting help to avoid burdening a benefactor^{34,54}, and gratitude motivating accepting help to build a communal relationship^{6,7}. However, because *U*_{Communal} = *U*_{Guilt} = *U*_{Gratitude} = ω_B in this formulation, there is no variability in the design for the model to be able to disentangle the effect of gratitude from that of guilt. To address this complexity, we constrain ϕ to be within the interval of [-1, 1], and explicitly divide up the parameter space such that $\phi > 0$ indicates a preference for gratitude and motives the

participants to accept the help, while $\phi < 0$ indicates a preference for guilt and motives the participants to reject the help.

$$\begin{cases} \phi_B > 0 \quad Gratitude \\ \phi_B < 0 \quad Guilt \end{cases}$$
(11)

Regardless of whether the participant is motivated primarily by guilt or gratitude, participants can still have a mixture of obligation captured by 1 - $|\phi|$, which ranges from [0, 1]. Unfortunately, if participants are equally sensitive to gratitude and guilt, ϕ will reduce to zero and the weight on obligation increases, which decreases the model fit and leads to some instability in the parameters.

See Supplementary Methods for the methods of model fitting, model comparison and parameter recovery for reciprocity decisions and help-acceptance decisions.

Data analyses in Study 3 (FMRI Study)

Univariate fMRI analyses. FMRI data preprocessing (see Supplementary Methods) and univariate analyses were conducted using Statistical Parametric Mapping software SPM12 (Wellcome Trust Department of Cognitive Neurology, London). We used a model-based fMRI analytic approach⁵⁹ to identify brain regions that parametrically tracked different components of the computational model for reciprocity during the Outcome period of the task (5s; Fig. 3b), where participants learned about the benefactor's decision to help. To ensure that each hypothesis tested had maximum variance, we chose to separately test each hypothesis using a separate model to minimize issues with multicollinearity. GLM 1 identified reciprocity related brain responses based on the parametric modulator of participant's reciprocity behavior D_B . GLM 2 identified brain responses related to communal concern based on the parametric modulator of the participant's appraisal of perceived care ω_{B} . GLM 3 identified brain responses related to obligation, which we modeled as a linear contrast of the participant's second-order belief of the benefactor's expectation for repayment $E_{B}^{\prime 54}$. For whole brain analyses, all results were corrected for multiple comparisons using cluster correction p < 0.05 with a cluster-forming threshold of p < 0.001, which attempts to control for family wise error (FWE) using Gaussian Random Field Theory¹⁰³. See Supplementary Methods for details of univariate fMRI analyses.

Meta-analytical decoding. To reveal the psychological components associated with the processing of reciprocity, communal concern and obligation, we conducted meta-analytic decoding using the Neurosynth Image Decoder⁶¹ (http://neurosynth.org). This allowed us to quantitatively evaluate the spatial similarity⁶⁰ between any Nifti-format brain image and selected meta-analytical images generated by the Neurosynth database (see Supplementary Methods).

Neural utility model of indebtedness. We constructed a neural utility model by combining our computational model for reciprocity with multivariate pattern analysis (MVPA) with our open source Python NLTools package¹⁰⁴ version 0.3.14 (https://nltools.org/)¹⁰⁵. First, using principal components regression with 5-fold cross-validation, we trained two separate multivariate whole-brain models predictive of communal concern (ω_B) and obligation (E_B'') terms in our behavioral model separately for each participant⁷¹⁻⁷³. For each whole-brain model, we extracted the cross-validated prediction accuracy (r value) for each participant, conducted r-to-z transformation, and then conducted a one-sample permutation *t*-test to evaluate whether each model was able to significantly predict the corresponding term. We used the cross-validated models to generate predictions for each trial for each participant and then used brain-predicted communal concern (ω_B) and obligation (E_B'') feelings as inputs to our computational model of reciprocity behavior (Model 1.1, Eq. 9) instead of the original terms. We estimated the θ values (i.e., weight on greed) and ϕ weighting parameters (i.e., relative trade-off between on communal concern and obligation) using the same procedure described in the behavioral computational modeling section. As a benchmark for our neural utility model, we used the same training procedure described above, but predicted trial-to-trial reciprocity behavior using principal components regression separately for each participant.

Finally, we were interested in evaluating how well we could estimate how much each participant had a relative preference for communal concern or obligation by computing the relative spatial alignment of their communal and obligation predictive spatial maps with their reciprocity predictive spatial map. We operationalized this relative pattern similarity as

relative pattern similarity = corr
$$\left(\overrightarrow{Obligation_{map}}, \overrightarrow{Reciprocity_{map}} \right)$$

-corr $\left(\overrightarrow{Commual_{map}}, \overrightarrow{Reciprocity_{map}} \right)$ (12)

We tested the Pearson correlation between this relative pattern similarity and the $(1 \cdot \phi)$ parameters estimated by fitting the computational model (Eq. 1) directly to the participants' behaviors. See Supplementary Methods for additional details about neural utility model.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Behavioral data from all the three studies are available on GitHub (https://github.com/xiaoxuepsy/Indebtedness) and Zenodo (https://doi.org/10.5281/zenodo.8328235)¹⁰⁶. The unthresholded first-level and second-level maps from the fMRI study are available on Open Science Framework (https://doi.org/10.17605/OSF.IO/K8RXH). Raw imaging data are available from the corresponding authors upon request due to privacy concern. Meta-analytic decoding was conducted using the meta-analytical images generated by the Neurosynth database (http:// neurosynth.org)⁶¹.

Code availability

The codes used in the current study are available on GitHub https://github.com/xiaoxuepsy/Indebtedness and Zenodo (https://doi.org/10.5281/zenodo.8328235)¹⁰⁶.

References

- Sherry, J. F. Jr Gift giving in anthropological perspective. J. Consum. Res. 10, 157–168 (1983).
- Carmichael, H. L. & MacLeod, W. B. Gift giving and the evolution of cooperation. Int. Econ. Rev. 38, 485–509 (1997).
- Nowak, M. A. & Sigmund, K. Evolution of indirect reciprocity. Nature 437, 1291–1298 (2005).
- Clark, M. S. & Mills, J. The difference between communal and exchange relationships: what it is and is not. *Pers. Soc. Psychol. Bull.* 19, 684–691 (1993).
- Clark, M. S. & Mills, J. R. A theory of communal (and exchange) relationships. in *Handbook of Theories of Social Psychology*. 2, 232–250 (Sage Publications Ltd, 2012).
- Algoe, S. B. Find, remind, and bind: the functions of gratitude in everyday relationships. Soc. Pers. Psychol. Compass 6, 455–469 (2012).
- Algoe, S. B., Haidt, J. & Gable, S. L. Beyond reciprocity: gratitude and relationships in everyday life. *Emotion* 8, 425 (2008).
- 8. Elfers, J. & Hlava, P. *The Spectrum of Gratitude Experience* (Springer, 2016).
- McCullough, M. E., Kilpatrick, S. D., Emmons, R. A. & Larson, D. B. Is gratitude a moral affect? *Psychol. Bull.* 127, 249 (2001).

Article

- Trivers, R. L. The evolution of reciprocal altruism. Q. Rev. Biol. 46, 35–57 (1971).
- 11. Neilson, W. S. The economics of favors. *J. Econ. Behav. Organ.* **39**, 387–397 (1999).
- 12. Akerlof, G. A. Labor contracts as partial gift exchange. *Q. J. Econ.* 97, 543–569 (1982).
- Greenberg, M. S. A theory of indebtedness. in Social Exchange. 3–26 (Springer, 1980).
- 14. Greenberg, M. S. & Westcott, D. R. Indebtedness as a mediator of reactions to aid. *N. Directions Helping* **1**, 85–112 (1983).
- 15. Regan, D. T. Effects of a favor and liking on compliance. J. Exp. Soc. Psychol. **7**, 627–639 (1971).
- 16. Kolm, S.-C. Reciprocity: An Economics of Social Relations (Cambridge University Press, 2008).
- Nadler, A. The other side of helping: Seeking and receiving help. in The Oxford Handbook of Prosocial Behavior. Oxford Library of Psychology. 307–328 (Oxford University Press, 2015).
- Fisher, J. D., Nadler, A. & Whitcher-Alagna, S. Recipient reactions to aid. *Psychol. Bull.* **91**, 27–54 (1982).
- 19. Fisher, J. New Directions in Helping: Recipient Reactions to Aid. Vol. 1 (Elsevier, 1983).
- Nadler, A., Mayseless, O., Peri, N. & Chemerinski, A. Effects of opportunity to reciprocate and self-esteem on help-seeking behavior. J. Pers. 53, 23–35 (1985).
- Watkins, P. C., Scheer, J., Ovnicek, M. & Kolts, R. The debt of gratitude: dissociating gratitude and indebtedness. *Cogn. Emot.* 20, 217–241 (2006).
- 22. Bal, A. Doctors and drug companies. *N. Engl. J. Med.* **352**, 733–734 (2005).
- 23. Malmendier, U. & Schmidt, K. You Owe Me (National Bureau of Economic Research, 2012).
- Fehr, E. & Gächter, S. Fairness and retaliation: the economics of reciprocity. J. Econ. Perspect. 14, 159–181 (2000).
- Gonzalez, B., & Chang, L. J. Computational models of mentalizing. in *The Neural Basis of Mentalizing*. 299–315 (Cham: Springer International Publishing, 2021).
- Falk, A., Fehr, E. & Fischbacher, U. On the nature of fair behavior. Econ. Ing. 41, 20–26 (2003).
- Sul, S., Guroglu, B., Crone, E. A. & Chang, L. J. Medial prefrontal cortical thinning mediates shifts in other-regarding preferences during adolescence. *Sci. Rep.* 7, 8510 (2017).
- Ellsworth, P. C. & Scherer, K. R. Appraisal processes in emotion. Handb. Affect. Sci. 572, V595 (2003).
- Frijda, N. H. The place of appraisal in emotion. Cogn. Emot. 7, 357–387 (1993).
- Frijda, N. H., Kuipers, P. & Ter Schure, E. Relations among emotion, appraisal, and emotional action readiness. J. Pers. Soc. Psychol. 57, 212 (1989).
- Lazarus, R. S. & Smith, C. A. Knowledge and appraisal in the cognition—emotion relationship. *Cogn. Emot.* 2, 281–300 (1988).
- 32. Scherer, K. R. Appraisal theory. in *Handbook of cognition and emotion*. 637–663 (John Wiley & Sons Ltd, 1999).
- 33. Smith, C. A. & Ellsworth, P. C. Patterns of cognitive appraisal in emotion. *J. Pers. Soc. Psychol.* **48**, 813 (1985).
- Battigalli, P. & Dufwenberg, M. Dynamic psychological games. J. Econ. Theory 144, 1–35 (2009).
- Battigalli, P., Corrao, R. & Dufwenberg, M. Incorporating beliefdependent motivation in games. J. Econ. Behav. Organ. 167, 185–218 (2019).
- Geanakoplos, J., Pearce, D. & Stacchetti, E. Psychological games and sequential rationality. *Games Econ. Behav.* 1, 60–79 (1989).
- Dufwenberg, M. & Kirchsteiger, G. A theory of sequential reciprocity. Games Econ. Behav. 47, 268–298 (2004).
- Rabin, M. Incorporating fairness into game theory and economics. Am. Econ. Rev. 83, 1281–1302 (1993).

- 39. Chang, L. J. & Smith, A. Social emotions and psychological games. *Curr. Opin. Behav. Sci.* **5**, 133–140 (2015).
- 40. Benedict, R. Chrysanthemum and the Sword. Patterns of Japanese Culture, Cleveland, New York (The World Publishing Company, 1946).
- 41. Kotani, M. Expressing gratitude and indebtedness: Japanese speakers' use of "I'm sorry" in English conversation. *Res. Lang.* Soc. *Interact.* **35**, 39–72 (2002).
- Naito, T. & Washizu, N. Note on cultural universals and variations of gratitude from an East Asian point of view. J. Behav. Sci. 10, 1–8 (2015).
- Washizu, N. & Naito, T. The emotions sumanai, gratitude, and indebtedness, and their relations to interpersonal orientation and psychological well-being among Japanese university students. *Int. Perspect. Psychol. Res. Pract. Consult.* 4, 209 (2015).
- Baumeister, R. F., Stillwell, A. M. & Heatherton, T. F. Guilt: an interpersonal approach. *Psychol. Bull.* **115**, 243–267 (1994).
- 45. Le, B. M., Impett, E. A., Lemay, E. P. Jr, Muise, A. & Tskhay, K. O. Communal motivation and well-being in interpersonal relationships: an integrative review and meta-analysis. *Psychol. Bull.* **144**, 1–25 (2018).
- 46. Naito, T. & Sakata, Y. Gratitude, indebtedness, and regret on receiving a friend's favor in Japan. *Psychologia* **53**, 179–194 (2010).
- 47. Tsang, J. A. The effects of helper intention on gratitude and indebtedness. *Motiv. Emot.* **30**, 199–205 (2006).
- Rotella, A., Sparks, A. M. & Barclay, P. Feelings of obligation are valuations of signaling-mediated social payoffs. *Behav. Brain Sci.* 43, e85 (2020).
- 49. Tomasello, M. The moral psychology of obligation. *Behav. Brain Sci.* **43**, e56 (2020).
- 50. Beeler-Duden, S., Yucel, M. & Vaish, A. The role of affect in feelings of obligation. *Behav. Brain Sci.* **43**, e60 (2020).
- Theriault, J. E., Young, L. & Barrett, L. F. The sense of should: a biologically-based framework for modeling social pressure. *Phys. Life Rev.* 36, 100–136 (2021).
- 52. Fehr, E. & Schmidt, K. M. A theory of fairness, competition, and cooperation. Q. J. Econ. **114**, 817–868 (1999).
- Blei, D. M. & Lafferty, J. D. Dynamic topic models. in Proceedings of the 23rd international conference on Machine learning. 113–120 (Association for Computing Machinery, 2006).
- Chang, L. J., Smith, A., Dufwenberg, M. & Sanfey, A. G. Triangulating the neural, psychological, and economic bases of guilt aversion. *Neuron* 70, 560–572 (2011).
- van Baar, J. M., Chang, L. J. & Sanfey, A. G. The computational and neural substrates of moral strategies in social decision-making. *Nat. Commun.* **10**, 1–14 (2019).
- Browne, M. W. & Cudeck, R. Alternative ways of assessing model fit. Sociol. Methods Res. 21, 230–258 (1992).
- Hu, L. T. & Bentler, P. M. Evaluating model fit. in Structural equation modeling: Concepts, issues, and applications. 76–99 (Sage Publications, 1995).
- West, S. G., Taylor, A. B. & Wu, W. Model fit and model selection in structural equation modeling. in *Handbook of structural equation* modeling. 1, 209–231 (The Guilford Press, 2012).
- 59. O'doherty, J. P., Hampton, A. & Kim, H. Model-based fMRI and its application to reward learning and decision making. *Ann. N. Y. Acad. Sci.* **1104**, 35–53 (2007).
- 60. Chang, L. J., Yarkoni, T., Khaw, M. W. & Sanfey, A. G. Decoding the role of the insula in human cognition: functional parcellation and large-scale reverse inference. *Cereb. Cortex* **23**, 739–749 (2013).
- Yarkoni, T., Poldrack, R. A., Nichols, T. E., Van Essen, D. C. & Wager, T. D. Large-scale automated synthesis of human functional neuroimaging data. *Nat. Methods* 8, 665 (2011).
- 62. Fox, G. R., Kaplan, J., Damasio, H. & Damasio, A. Neural correlates of gratitude. *Front. Psychol.* **6**, 1491 (2015).

- Yu, H., Cai, Q., Shen, B., Gao, X. & Zhou, X. Neural substrates and social consequences of interpersonal gratitude: Intention matters. *Emotion* 17, 589–601 (2017).
- Yu, H., Gao, X., Zhou, Y. & Zhou, X. Decomposing gratitude: Representation and integration of cognitive antecedents of gratitude in the brain. J. Neurosci. 38, 4886–4898 (2018).
- Cooper, J. C., Kreps, T. A., Wiebe, T., Pirkl, T. & Knutson, B. When giving is good: ventromedial prefrontal cortex activation for others' intentions. *Neuron* 67, 511–521 (2010).
- 66. Ruff, C. C. & Fehr, E. The neurobiology of rewards and values in social decision making. *Nat. Rev. Neurosci.* **15**, 549 (2014).
- Koban, L., Corradi-Dell'Acqua, C. & Vuilleumier, P. Integration of error agency and representation of others' pain in the anterior insula. J. Cogn. Neurosci. 25, 258–272 (2013).
- Yu, H., Hu, J., Hu, L. & Zhou, X. The voice of conscience: neural bases of interpersonal guilt and compensation. Soc. Cogn. Affect. Neurosci. 9, 1150–1158 (2014).
- 69. Hampton, A. N., Bossaerts, P. & O'Doherty, J. P. Neural correlates of mentalizing-related computations during strategic interactions in humans. *Proc. Natl Acad. Sci. USA* **105**, 6741–6746 (2008).
- Van Overwalle, F. & Baetens, K. Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. *Neuroimage* 48, 564–584 (2009).
- Woo, C. W., Chang, L. J., Lindquist, M. A. & Wager, T. D. Building better biomarkers: brain models in translational neuroimaging. *Nat. Neurosci.* 20, 365–377 (2017).
- Chang, L. J., Gianaros, P. J., Manuck, S. B., Krishnan, A. & Wager, T. D. A sensitive and specific neural signature for picture-induced negative affect. *PLoS Biol.* **13**, e1002180 (2015).
- Wager, T. D. et al. An fMRI-based neurologic signature of physical pain. N. Engl. J. Med. 368, 1388–1397 (2013).
- Kriegeskorte, N., Mur, M. & Bandettini, P. A. Representational similarity analysis-connecting the branches of systems neuroscience. *Front. Syst. Neurosci.* 2, 4 (2008).
- Mathews, M. A. & Green, J. D. Looking at me, appreciating you: Self-focused attention distinguishes between gratitude and indebtedness. *Cogn. Emot.* 24, 710–718 (2010).
- Lench, H. C., Flores, S. A. & Bench, S. W. Discrete emotions predict changes in cognition, judgment, experience, behavior, and physiology: a meta-analysis of experimental emotion elicitations. *Psychol. Bull.* **137**, 834–855 (2011).
- Lindquist, K. A., Siegel, E. H., Quigley, K. S. & Barrett, L. F. The hundred-year emotion war: are emotions natural kinds or psychological constructions? Comment on Lench, Flores, and Bench (2011). *Psychol. Bull.* **139**, 255–263 (2013).
- 78. Larsen, R. J. & Fredrickson, B. L. in *Well-being: The Foundations of Hedonic Psychology*. 40–60 (Russell Sage Foundation, 1999).
- 79. Nisbett, R. E. & Wilson, T. D. Telling more than we can know: verbal reports on mental processes. *Psychol. Rev.* **84**, 231–259 (1977).
- Jolly, E. & Chang, L. J. The flatland fallacy: moving beyond lowdimensional thinking. *Top. Cogn. Sci.* 11, 433–454 (2019).
- Chang, L. J. & Jolly, E. Emotions as computational signals of goal error. in *The nature of emotion: Fundamental questions*. 343–348 (Oxford University Press, 2018).
- Xiang, T., Lohrenz, T. & Montague, P. R. Computational substrates of norms and their violations during social exchange. *J. Neurosci.* 33, 1099–1108a (2013).
- 83. Gao, X. et al. Distinguishing neural correlates of contextdependent advantageous- and disadvantageous-inequity aversion. *Proc. Natl Acad. Sci. USA* **115**, E7680–E7689 (2018).
- 84. Khalmetski, K., Ockenfels, A. & Werner, P. Surprising gifts: theory and laboratory evidence. *J. Econ. Theory* **159**, 163–208 (2015).
- 85. Battigalli, P., Dufwenberg, M. & Smith, A. Frustration and Anger in Games. *CESifo*. CESifo Working Paper Series 5258 (2015).

- Chang, L. J. & Sanfey, A. G. Great expectations: neural computations underlying the use of social norms in decision-making. Soc. *Cogn. Affect. Neurosci.* 8, 277–284 (2013).
- Krajbich, I., Adolphs, R., Tranel, D., Denburg, N. L. & Camerer, C. F. Economic games quantify diminished sense of guilt in patients with damage to the prefrontal cortex. *J. Neurosci.* 29, 2188–2192 (2009).
- Smith, A., Bernheim, B. D., Camerer, C. & Rangel, A. Neural activity reveals preferences without choices. *Nber Working Pap.* 6, 1–36 (2014).
- 89. Knutson, B., Rick, S., Wimmer, G. E., Prelec, D. & Loewenstein, G. Neural predictors of purchases. *Neuron* **53**, 147–156 (2007).
- Hein, G., Morishima, Y., Leiberg, S., Sul, S. & Fehr, E. The brain's functional network architecture reveals human motives. *Science* 351, 1074–1078 (2016).
- 91. Haidt, J. The moral emotions. *Handb. Affect. Sci.* **11**, 852–870 (2003).
- Fiske, A. P. The four elementary forms of sociality: framework for a unified theory of social relations. *Psychol. Rev.* 99, 689–723 (1992).
- 93. Rai, T. S. & Fiske, A. P. Moral psychology is relationship regulation: moral motives for unity, hierarchy, equality, and proportionality. *Psychol. Rev.* **118**, 57–75 (2011).
- Fiske, A. P. Socio-moral emotions motivate action to sustain relationships. Self Identity 1, 169–175 (2002).
- Earp, B. D., McLoughlin, K. L., Monrad, J. T., Clark, M. S. & Crockett, M. J. How social relationships shape moral wrongness judgments. *Nat. Commun.* 12, 5776 (2021).
- van Baar, J. M., Klaassen, F. H., Ricci, F., Chang, L. J. & Sanfey, A. G. Stable distribution of reciprocity motives in a population. *Sci. Rep.* 10, 18164 (2020).
- 97. Yu, H. et al. A generalizable multivariate brain pattern for interpersonal guilt. *Cereb. Cortex* **30**, 3558–3572 (2020).
- Neto, J. L., Santos, A. D., Kaestner, C. A., & Freitas, A. A. Document clustering and text summarization. in *Proceedings of the 4th International Conference Practical Applications of Knowledge Discovery and Data Mining*. 41–55 (The Practical Application Company, 2000).
- Salton, G. & Buckley, C. Term-weighting approaches in automatic text retrieval. *Inform. Process. Manag.* 24, 513–523 (1988).
- Blei, D. M., Ng, A. Y. & Jordan, M. I. Latent dirichlet allocation. J. Mach. Learn. Res. 3, 993–1022 (2003).
- Fabrigar, L. R., Wegener, D. T., MacCallum, R. C. & Strahan, E. J. Evaluating the use of exploratory factor analysis in psychological research. *Psychol. Methods* 4, 272–299 (1999).
- 102. Greenberg, M. S. & Shapiro, S. P. Indebtedness: an adverse aspect of asking for and receiving help. *Sociometry* **34**, 290–301 (1971).
- Woo, C.-W., Krishnan, A. & Wager, T. D. Cluster-extent based thresholding in fMRI analyses: pitfalls and recommendations. *Neuroimage* **91**, 412–419 (2014).
- 104. Chang, L. J. et al. cosanlab/nltools: 0.4.7 (v0.4.7). Zenodo https:// doi.org/10.5281/zenodo.7015135 (2022).
- Haynes, J.-D. & Rees, G. Neuroimaging: decoding mental states from brain activity in humans. *Nat. Rev. Neurosci.* 7, 523 (2006).
- Gao, X. et al. The psychological, computational, and neural foundations of indebtedness. *Zenodo* https://doi.org/10.5281/ zenodo.8328235 (2023).

Acknowledgements

We thank Drs. Matthew Rushworth and Christian C. Ruff for their comments and suggestions on this article. In addition, we thank Ms. Wan Wang, Mr. Shuaiqi Li and Mr. Sensen Song for their assistances in data collection, Ms. Yunyan Duan for her advice in topic modeling, and Ms. Zhewen He for the preparation of the manuscript. Dr. Gao thanks Dr. Can Tang, Dr. Li Zhang, Ms. Jiyan Lyu, and Ms. Kewalin Boonsatta for their support during the revision process. This work was supported by National Natural Science Foundation of China (71942001, X.Z. and X.G.; 32371094, 31900798, X.G.; 31630034, X.Z. and X.G.), Young Elite Scientists Sponsorship Program by China Association for Science and Technology (YESS20210176, 2021QNRC001, X.G.), the National Science Foundation of USA (CAREER 1848370, L.J.C.), the National Institute of Health (R01MH116026, L.J.C.), the Research Project of Shanghai Science and Technology Commission (20dz2260300, X.G. and X.Z.), the Fundamental Research Funds for the Central Universities (X.G. and X.Z.), and the STI 2030 - Major Projects 2021ZD0200500 (X.Z. and X.G.). We also acknowledge support from the Graduate School of Peking University to fund Dr. Gao's training at Dartmouth College.

Author contributions

X.G., E.J., H.Y., X.Z., and L.J.C. designed the experiments. X.G. and H. L. implemented the study design and collected the data. X.G. and L.J.C. carried out the analyses. X.G., E.J., H.Y., X.Z., and L.J.C. wrote the paper. X.Z. and L.J.C. supervised the work. All authors provided critical revisions and approved the final paper for submission.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41467-023-44286-9.

Correspondence and requests for materials should be addressed to Xiaoxue Gao, Xiaolin Zhou or Luke J. Chang.

Peer review information *Nature Communications* thanks Grit Hein, Christoph Korn, Rebecca Saxe and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. A peer review file is available.

Reprints and permissions information is available at http://www.nature.com/reprints

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit http://creativecommons.org/ licenses/by/4.0/.

© The Author(s) 2024