

The effects of gratitude expression on neural activity



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ABSTRACT

Gratitude is a common aspect of social interaction, yet relatively little is known about the neural bases of gratitude expression, nor how gratitude expression may lead to longer-term effects on brain activity. To address these twin issues, we recruited subjects who coincidentally were entering psychotherapy for depression and/or anxiety. One group participated in a gratitude writing intervention, which required them to write letters expressing gratitude. The therapy-as-usual control group did not perform a writing intervention. After three months, subjects performed a “Pay It Forward” task in the fMRI scanner. In the task, subjects were repeatedly endowed with a monetary gift and then asked to pass it on to a charitable cause to the extent they felt grateful for the gift. Operationalizing gratitude as monetary gifts allowed us to engage the subjects and quantify the gratitude expression for subsequent analyses. We measured brain activity and found regions where activity correlated with self-reported gratitude experience during the task, even including related constructs such as guilt motivation and desire to help as statistical controls. These were mostly distinct from brain regions activated by empathy or theory of mind. Also, our between groups cross-sectional study found that a simple gratitude writing intervention was associated with significantly greater and lasting neural sensitivity to gratitude – subjects who participated in gratitude letter writing showed both behavioral increases in gratitude and significantly greater neural modulation by gratitude in the medial prefrontal cortex three months later.

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Introduction

Gratitude is an essential part of human prosocial behavior. A number of recent studies have shown the benefits of gratitude interventions on well being, mainly using gratitude letter writing or keeping a gratitude diary, both of which can be effective (Kaczmarek et al., 2015). Gratitude interventions have recently been shown as effective at increasing well being in students (Flinchbaugh et al., 2012), those with chronic pain (Baxter et al., 2012), depression (Cheng et al., 2015), and older adults (Killen and Macaskill, 2015). Gratitude interventions have similar effectiveness compared with mindfulness interventions (O’Leary and Dockray, 2015) and practicing kindness (Kerr et al., 2015).

Despite the recent findings regarding gratitude intervention effectiveness, the basic neural mechanisms involved in gratitude are relatively unknown, as are the neurological mechanisms mediating the effects of gratitude interventions (Layous et al., 2011). On the one hand, gratitude may involve *affective* processes. Gratitude has been characterized as a positive moral affect alongside other moral affects such as empathy, sympathy, guilt, and shame, and as a force that helps people maintain positive social reciprocity (McCullough et al., 2001). On the other hand, other work has cast gratitude as related to a more *cognitive* process of benefit appraisal (Wood et al., 2008).

Gratitude may also be delineated in terms of *experience* vs. *expression*. The recipients (or observers) of a generous or prosocial act may experience emotions related to gratitude, such as positive affect, empathy, and increased inclination toward prosocial behavior (Emmons and Stern, 2013). The experience of gratitude may naturally lead to an expression of gratitude, which typically takes the form of a verbal recognition (“thank you”) or a reciprocal gift (such as generous restaurant tipping). In this paper we address both experience and expression of gratitude in three inter-related ways. First, subjects in an experimental group express gratitude in the form of a written letter three months prior to fMRI scanning. Second, during scanning, we model gratitude as an expression, with monetary gifting as a quantifiable operationalization of gratitude expression. Third, during scanning, we also ask subjects to evaluate their experience of gratitude on each trial, with self-reports on a Likert scale.

Gratitude has been studied with neuroimaging as part of more general investigations of human social value (Zahn et al., 2009), but the specific neural correlates of gratitude have only recently been explored (Fox et al., 2015). A number of similar social cognitive and affective constructs have been studied, including trust and reciprocity (King-Casas et al., 2005), fairness (De Quervain et al., 2004; Sanfey et al., 2003), and empathy (Singer et al., 2004, 2006). Collectively these studies highlight a number of brain regions as central to social interaction, including prominently the anterior cingulate cortex (ACC), anterior insula (AI), ventromedial prefrontal cortex (vmPFC), and striatum, which are generally limbic regions associated with affect and valuation. The anterior

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cingulate cortex in particular may play a key role in predicting and evaluating the outcomes of actions (Alexander and Brown, 2010, 2011), including in social contexts (Chiu et al., 2008; King-Casas et al., 2005; Tomlin et al., 2006). ACC activity reflects and drives avoidance behavior, especially of potential losses (Brown and Braver, 2007; Fukunaga et al., 2012) as well as potential regret (Coricelli et al., 2005) and social affect (Harris et al., 2007), and has been shown to correlate with empathy (Rameson et al., 2012), especially for pain (Singer et al., 2006). If gratitude involves primarily an affective process, then gratitude expression should correlate with activity in the limbic regions.

Gratitude may also involve cognitive processes, including computations and appraisals of appropriate reciprocity (Wood et al., 2008). Mental calculations generally involve more dorsolateral prefrontal and parietal brain regions (Dehaene et al., 2004). Thus, if gratitude involves more cognitive than affective processes, then gratitude expression should correlate with activity in the parietal and dorsolateral prefrontal regions.

In addition to questions about the basic neural mechanisms of gratitude, there is potential clinical relevance. Growing evidence supports the mental health benefits of gratitude interventions (e.g. Boehm et al., 2011; Emmons and McCullough, 2003; Froh et al., 2008; Lyubomirsky et al., 2011; Seligman et al., 2005; Sheldon and Lyubomirsky, 2006; Watkins et al., 2003). Research on such interventions has focused mainly on non-clinical populations (e.g., college and high school students). Still, the basic neural mechanisms through which gratitude interventions might positively influence mental health are not well understood. Several mechanisms have been proposed (Emmons and Mishra, 2012; Geraghty et al., 2010) but only one peer-reviewed study so far has identified a mediator (i.e., feelings of gratitude) of the positive effects of a gratitude intervention (Emmons and McCullough, 2003).

Here our aim is to elucidate specifically the basic neural correlates of gratitude expression, and we do not investigate or report clinical effects. Our study focuses on four related questions: first, what are the immediate neural activity correlates associated with acts of expressing gratitude (operationalized as monetary gifts)? Second, is the neural activity more consistent with gratitude as a cognitive process or as an emotional process? Third, to what extent does gratitude expression involve the brain regions associated with empathy and theory of mind processes? Fourth, what are the long-term effects of written gratitude expression (as distinct from grateful monetary gifting) on neural sensitivity to gratitude?

To address these questions, we developed a variant of the trust game (Berg et al., 1995), called the “Pay It Forward” task, in which subjects express gratitude as monetary gifts while undergoing fMRI. We administered a short gratitude writing intervention to half of the subjects and explored the effect of that intervention on brain activity during the gratitude task several months later. This approach allows us to measure both the immediate neural activity associated with gratitude and the lasting effects of gratitude expression on brain activity. Here we show two main results: first, that gratitude correlates with activity in specific set of brain regions; and second, that a simple gratitude writing intervention is associated with significant increases in both gratefulness and neural sensitivity to gratitude over the course of weeks to months.

Methods

Subject recruitment

Subjects were recruited from a population of psychotherapy clients seeking clinical counseling. All subjects provided written informed consent, and all procedures were approved by the Indiana University IRB. Subjects were randomized to one of three conditions: a gratitude writing intervention, an expressive writing intervention, or a psychotherapy-only condition. The randomization was performed with successive subjects to keep the running group sizes as equal as possible, without regard for particular demographic factors.

Subjects initially completed the six-item Gratitude Questionnaire (GQ) (McCullough et al., 2002), the three-item gratitude adjectives scale (GAC3) (McCullough et al., 2002), which assess self-reports of how grateful one feels in daily life, and the BHM-20 scale, which briefly assesses mental health, including anxiety and depression (Kopta and Lowry, 2002). Higher BHM-20 scores reflect better mental health. For the gratitude writing intervention, subjects were asked to spend 20 min writing a letter to someone expressing gratitude. They did this during three consecutive sessions on the first, second, and third week of counseling. They were instructed that they could choose whether or not to actually send the letters to the recipient. Subjects in the expressive writing condition were asked to write about their most stressful episodes in life. Three months after counseling, the gratitude writing and psychotherapy-only subjects were recruited to participate in the fMRI task.

A total of 43 clients (22 in the gratitude intervention condition and 21 in the psychotherapy only condition, age range 18 to 34, mean 22.98, 32 females, all right handed) were recruited for the fMRI study. We did not scan the expressive writing subjects for cost reasons, although future studies might consider doing so as an additional control. The subject demographics are summarized in Table 1. There was no difference between the fMRI gratitude writing vs. psychotherapy-only groups with respect to their age ($p=0.50$), gender ($p=0.73$) initial GQ (trait gratitude) scores ($p=0.41$), or symptoms of anxiety/depression as measured on the BHM-20 symptom subscale ($p=0.55$). The average BHM-20 score at intake was 2.39 for the gratitude group and 2.50 for the therapy-as-usual group (Table 1), which is consistent with average scores of 2.33 for psychotherapy outpatients and 2.68 for college counseling clients, as reported by the BHM-20 developer (Kopta and Lowry, 2002), who also reported for comparison that the average healthy college student BHM-20 score was 3.13 ($SD=0.51$). Lower BHM-20 scores indicate more symptoms of anxiety and/or depression.

fMRI task

In order to perform the study in a controlled setting, the expression of gratitude was operationalized as money, with a function similar to tipping a restaurant server. To partly dissociate gratitude from guilt aversion, we modified the trust game (Berg et al., 1995) to make it a “Pay It Forward” (PIF) task (Fig. 1). In the PIF task, subjects acted as a Trustee, who received a sum of money between \$1 and \$20 from a benefactor, whose picture was shown on the screen. Subjects were told that the benefactor was a real person, not a computer, although the endowments were in fact determined by a computer. The subjects were then shown a potential third party beneficiary, with whom the trustee could share any portion of the endowment given by the benefactor. They were told that the benefactor did not want the money back, but that the benefactor wanted them to pass on what they had received if they felt that they wanted to express gratitude for the endowment. The beneficiary was said to not have immediate need of the money, but would nevertheless appreciate it. We could have quantified gratitude simply as a Likert rating, but we chose not to. Instead, we chose to operationalize gratitude here as money given, for several reasons. First, it renders gratitude quantifiable in terms of monetary value, which is necessary for the quantitative analyses we perform. Second,

Table 1

Demographics. Subjects showed no significant differences between groups regarding age, gender, initial gratitude (GQ), or initial anxiety/depression symptoms (BHM-20).

Variable	Gratitude	Control	P
Gender	F = 17, M = 5	F = 15, M = 6	0.73 (Fisher exact 2 sided)
Age (range 18–34)	23.41	22.52	0.50 (2 tailed)
GQ	5.38	5.67	0.41 (2 tailed)
Symptoms (initial BHM-20)	2.39	2.50	0.55 (2 tailed)

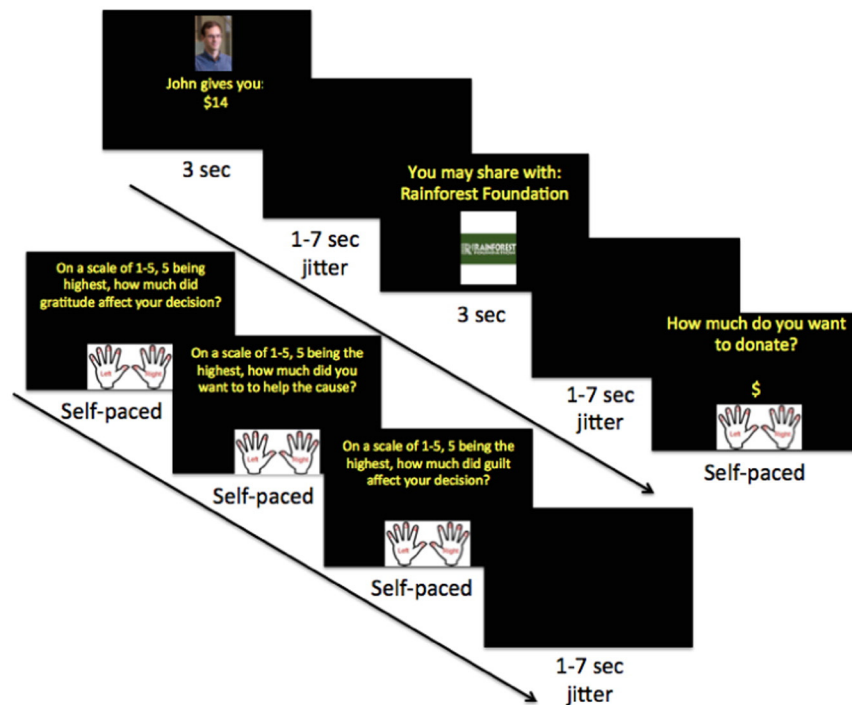


Fig. 1. The “Pay It Forward” task. Each trial of the task began with a benefactor, who endowed the subject with a dollar value between \$1 and \$20. After a variable delay, the subject was shown a charitable cause (person or organization) to which they could donate. They were told that the benefactor requested them to donate to the charity to the extent that they appreciated the benefactor’s gift. Subjects were then given an opportunity to type in a donation amount. Then they were asked to rate on a Likert scale how much the factors of gratitude, desire to help the cause, and guilt influenced their decision about how much to give. All jittered delays lasted between 1 and 7 seconds, with an average of 2.14 s, exponentially distributed. A wide range of charities and benefactor ethnicities were used in the experiment in order to maximize the variance in the responses. One response from each subject was chosen to be actually paid – the subject was given the amount of money they chose to keep, and the donation amount was given to the charity.

we reasoned that a costly expression of gratitude was more likely to engage the subjects than a cost-free expression, such as a Likert rating of experienced gratitude. Third, monetary gifts as expressions of gratitude are ecologically valid as for example in tipping restaurant servers, with the caveat that our task here involves payment to a third party rather than reciprocity to the benefactor. Of note, we still measured the self-reported experience of gratitude separately on each trial as described below.

Subjects were placed in the fMRI scanner and performed repeated iterations of the PIF task. They performed five runs of 7.5-minute fMRI blocks. Each trial began with one of ten possible benefactor faces and names, 5 male and 5 female with neutral levels of emotional expression (Fig. 1). The fictitious benefactor’s name appeared above the face, and the amount of the endowment for the trial was displayed below the benefactor’s face. The endowment range was between \$1 and \$20 for each trial. The endowment value was visible for 3 seconds followed by a blank screen for a jittered interval with a minimum of 1 second duration, followed by a potential beneficiary, with the fictitious name of the beneficiary above. The beneficiary was one of eight possibilities, either a fictitious person, (neutral emotional expression, $p = 0.5$ female, $p = 0.5$ Caucasian), or a politically neutral charity (Aid for Africa, Indiana Wildlife Federation, Mother Hubbard’s Kitchen, or the Rainforest Foundation). The beneficiary was visible for 3 seconds followed by a jittered interval of a minimum one second duration, followed by a cue to select a donation amount. Once subjects selected a donation amount via button presses, they were asked to rate on 5-point Likert scale their a) gratitude motivation, (b) their desire to help the particular beneficiary, (c) their guilt motivation. The order of these three questions was consistent across trials, i.e. not counterbalanced, for two reasons. First, we wanted to ensure that gratitude self-report was always first and thus not contaminated by order effects from subsequent questions. Second, the consistent order of the remaining two questions made them more predictable, which we expected would reduce confusion about the questions and lower reaction times. This mattered because the

responses were self-paced in order to ensure that subjects provided a response to all self-report questions on all trials. The tradeoff with our design choice is that we cannot rule out order effects of the self-report question responses. Still, the self-paced design maximizes trial yield while ensuring that subjects answer every question. For validity, subjects were informed that one of their interactions would be chosen at random and actually paid out according to their choices, with the designated gift going to the charity and the remaining portion being paid to the subject. We did in fact choose one of each subject’s choices and pay it to the designated charity, except that when the beneficiary was an individual, then the money went to a charitable organization instead for purposes of accountability. After the self report phase of each trial there was a jittered interval with a minimum one second duration until the start of the following trial. Each run began with and ended with 15 seconds of blank screen to establish a baseline of neural activity. There were 27 trials per block, which led to 135 trials per subject.

We counterbalanced the order of button presses across subjects, so that for half of the subjects, the left hand pressed buttons 1 (little finger) through 5 (thumb), and for the other half of subjects, the left hand pressed buttons 0 (little finger), 9 (ring finger), 8 (middle finger), 7 (index finger), and 6 (thumb). The finger-to-button mapping was presented visually to the subjects during the experiment. This motor counterbalancing avoids potential confounds between motor-related activation and higher-level factors such as gratitude, guilt, and desire to help, allowing the motor activation to load instead on motor regressors at the time of button press. Subjects indicated the amount of money they wished to give by pressing two buttons in succession, corresponding to the tens and ones places of the number of dollars they wished to give.

fMRI methods and analysis

Images were acquired on a 3T Siemens TIM Trio scanner using a 32-channel head coil. Functional BOLD data were collected at a 30° angle

from the anterior commissure–posterior commissure line in order to maximize signal-to-noise ratio in the orbital and ventral regions of the brain (Deichmann et al. 2003). Functional T2*-weighted images were acquired using a gradient echo planar imaging sequence with 35 axial slices and $3.44 \times 3.44 \times 3.8$ mm voxels; TR = 2000 ms; TE = 25 ms; 64×64 voxel matrix; flip angle = 70; field of view = $220\text{mm} \times 220\text{mm}$. High resolution T1-weighted MPRAGE images were collected for spatial normalization consisting of 160 sagittal slices ($256 \times 256 \times 160$ voxel matrix of $1 \times 1 \times 1$ mm voxels, TR = 1800 ms; TE = 2.67 ms; flip angle = 9) at the end of each session.

Functional data were spike-corrected on a voxel-by-voxel basis to reduce the impact of artifacts using AFNI's 3dDespike (<http://afni.nimh.nih.gov/afni>). Subsequent preprocessing was done using SPM5 (Wellcome Department of Imaging Neuroscience London, UK; www.fil.ion.ucl.ac.uk/spm/). Functional images were coregistered for differences in slice timing using sinc-interpolation (Oppenheim et al., 1999) and head movement using a least-squares approach and a 6 parameter rigid body spatial transformation. Once the resulting images were coregistered to the structural image and normalized to the SPM standard 152T1 atlas template Montreal Neurological Institute (MNI) space using the standard SPM5 normalization functions with both affine and nonlinear warping, the resulting functional images were then spatially smoothed with an 8-mm³ full-width-at-half-maximum isotropic Gaussian kernel. Functional neuroimaging data were statistically analyzed based on a general linear model (GLM) with random effects implemented in SPM5. Each individual subject's GLM was estimated with a canonical hemodynamic response function with no derivatives, a microtime resolution of 16 time bins per scan, a high-pass filter cutoff of 128 seconds using a residual forming matrix, autoregressive AR(1) to account for serial correlations, and restricted maximum likelihood (ReML) for model estimation.

For each subject, we constructed GLMs with the aim of measuring the processes involved in the decision to express a level of gratitude with a monetary gift. We included one regressor for each of the following event types, each with events modeled as having zero duration: the onset of the endowment event, the onset of the beneficiary information, the onset of the decision time (i.e. the prompt to enter a donation amount), the onset of the first button press (when subjects indicated how much they wanted to “pay forward”), the onset of the second button press (again for how much to pay forward), the onset of the gratitude rating button press (a single digit on a Likert scale), the onset of the desire to help rating button press (also on a Likert scale), and the onset of the guilt motivation rating button press (also on a Likert scale). Although the information about which button was pressed provided valuable information (and that information was recorded), the motor-related activity of the button press itself was unimportant, so the button press regressors were largely nuisance regressors to account for motor-related activation that was not of interest. In addition, we added four parametrically modulated (PM) regressors, with zero-duration events modeled at the onset of the decision time. The height of each modeled event was determined by the corresponding PM, which was mean-centered for each subject. These PM regressors were independent of the button press response regressors, because the PM regressors were mean-centered and parametrically modulated, and they occurred at somewhat different times. The varying parametric modulation across events decorrelates the PM regressors from regressors that model the main effect of an event. The first PM was the gratitude rating; the second was the guilt rating; the third was the desire to help rating, and the fourth was the percent of the initial endowment actually given. These PM regressors afforded an estimate of how much each self-reported emotion correlated with activity at the time of decision. We were primarily interested in the gratitude PM regressor, while the others served as statistical controls. It is important to note that the order matters when entering the PM, because successive PMs are orthogonalized with respect to the preceding ones. This means

that the first PM regressor entered has priority in accounting for any variance shared with subsequent regressors. We also included motion regressors for those subjects (eight in total) who had more than 3 mm total movement across a session or 0.5 mm from one image acquisition to another. In that case, we included 24 motion regressors, using a Volterra expansion (Friston et al., 1996): the six degrees of freedom including three for translation and three for rotation, the squared values of the six degrees of freedom, the scan-to-scan difference (i.e. time derivative) of the six motion regressors, and the squared values of the six time derivative regressors. Selectively including motion regressors for subjects with substantial movement maximizes the sensitivity to real effects while minimizing the spurious effects of motion (Johnstone et al., 2006). GLM regressor contrasts were computed for each subject and then evaluated with random effects tests at the population level. Unless otherwise noted, we analyzed each regressor across the population by looking at the whole brain, with an initial threshold of $p < 0.001$, and we report as significant those regions which further passed a cluster-correction for multiple comparisons with $p < 0.05$, using SPM5 standard cluster correction based on random field theory.

Results

The gratitude writing intervention led to better clinical outcomes in a larger cohort of subjects than we analyze here, but there were no significant differences in clinical outcomes between the therapy-as-usual control group and the gratitude group fMRI subjects here, as we elaborate below. We treat the clinical questions and results more fully in a separate paper (Wong et al., in preparation). Briefly, in a larger cohort of several hundred subjects, those in the gratitude writing condition (including all subjects, both those that were fMRI participants and those that were not) reported significantly better mental health than those in the expressive writing and therapy-as-usual control conditions about 4 weeks and 12 weeks after the conclusion of the writing interventions. Additionally, when the gratitude writing condition was compared to the expressive writing condition, a lower proportion of negative emotion words in subjects' writing mediated the effect of condition on mental health. That is, subjects in the gratitude writing condition used a lower percentage of negative words than those in the expressive writing condition, which was in turn associated with better mental health. Detailed information about these findings are described in a separate manuscript (Wong et al., in preparation).

With regard to only the subjects who participated in the present fMRI study, we found no significant differences in the clinical outcomes of those in the gratitude group vs. those in the therapy-as-usual control group. We compared the difference in BHM-20 scores one week after the writing sessions relative to intake (two weeks before completion of all the writing sessions). The gratitude subjects showed a trend of greater improvement relative to therapy-as-usual controls, but this was not significant (Gratitude group increase = 0.36, Control group increase = 0.17, $t(39) = 1.44$, $p = 0.08$, one-tail). However, the gratitude subjects did show a greater increase in gratitude (GAC) scores relative to therapy-as-usual controls at one week after the writing sessions relative to intake (Gratitude = 1.27, Control = 0.06, $t(40) = 2.25$, $p = 0.015$, one-tail). This suggests that our gratitude writing intervention was effective at increasing gratitude in the fMRI subjects and provides a behavioral basis for the between groups fMRI effects shown below.

For the Pay It Forward task, subjects gave an average of 60.5% (range 18.4% to 91.5%) of their endowment on each trial to the beneficiaries, indicating that the task was effective in eliciting altruistic donations, and subjects neither gave all the money away nor kept it all for themselves. Also, the average gratitude rating across subjects was 2.71 (range 1 to 4.66), which was significantly greater than the minimum possible gratitude rating ($p < 0.001$). The average guilt rating was 2.41 (range 1 to 4.3), which was significantly greater than the minimum possible ($p < 0.001$). The average desire to help

rating was 2.97 (range 1.41 to 4.26), which likewise was significantly greater than the minimum possible ($p < 0.001$). All of these suggest that the subjects experienced gratitude, guilt, and desire to help as significant factors in their decisions.

Parametric modulators

We first collapsed across both intervention groups to explore whether the self-reported gratitude, guilt, and desire-to-help ratings were correlated within subjects. We found that the self-reported desire to help and guilt regressors were not correlated within a given subject (average $r = 0.01$, $t(42) = 0.14$, $p = 0.89$, Fishers r -to- Z transformed). The gratitude and desire-to-help ratings were positively correlated (average $r = 0.36$, $t(42) = 7.04$, $p < 10^{-7}$, Fishers r -to- Z transformed). The gratitude and guilt ratings were positively correlated as well (average $r = 0.10$, $t(42) = 2.3$, $p = 0.026$, Fishers r -to- Z transformed). The gratitude ratings and percent of endowment given were positively correlated (average $r = 0.21$, $t(42) = 4.53$, $p < 0.00005$, Fishers r -to- Z transformed). This suggests that gratitude was most closely associated with a desire to “Pay It Forward” to help the designated cause, and while guilt may have played some role, that role was less significant. These findings also suggest that brain activity correlating with a desire to help may share some variance with brain activity correlating with gratitude in this study, and *vice versa*. Furthermore, although the percent given was unsurprisingly correlated positively with the total amount given (average $r = 0.37$, $t(42) = 9.01$, $p < 10^{-10}$, Fishers r -to- Z transformed), there was apparently a ceiling effect – a larger initial endowment correlated negatively with the percent given (average $r = -0.23$, $t(42) = -6.50$, $p < 10^{-7}$, Fisher’s r -to- Z transformed), indicating that subjects were reluctant to give large absolute dollar amounts.

Neuroimaging

Across the population, the gratitude PM regressor loaded significantly positively on four regions (Fig. 2A): in the left superior parietal lobule, left superior frontal gyrus, left inferior frontal gyrus, and right middle occipital gyrus (Table 2), using an initial uncorrected threshold of $p < 0.001$ to identify regions and then a cluster-corrected threshold of $p < 0.05$ to determine which clusters were significant after correcting for multiple comparisons. We also explored whether any regions loaded negatively on the parametrically modulated gratitude rating regressor. With a slightly more liberal threshold of $p < 0.005$ for determining candidate clusters, we found several additional regions that passed cluster correction (Table 2), in the medial frontal gyrus, parietal lobe, and visual cortex. We further interrogated the limbic regions including the amygdala, ventral striatum, ventromedial prefrontal cortex, and insula, but we found no other significant loading on the gratitude rating regressor, either positively or negatively, even at an uncorrected threshold of $p < 0.001$.

For the Guilt PM regressor, there were no brain regions that passed correction. For the Desire to help PM regressor, there were four brain regions that reached significance, in the left mid-occipital region, left precentral gyrus (BA6), left superior parietal lobule (BA7), and left cerebellar declive (Fig. 2B, Table 3).

Since the gratitude rating regressor was entered first, it had priority for accounting for the variance in the BOLD signal at the time of decisions. We tested how robust the gratitude effect was by constructing two additional GLMs: the “guilt-then-gratitude” GLM was identical to the original GLM, except that we entered the guilt regressor first, and then gratitude (followed by desire to help, then percent given). This affords a test of the gratitude effect while “partialing out” the effects of guilt. The gratitude effect cluster remained significant in the left superior parietal lobule (MNI $-22, -58, 54$; $p < 0.001$, cluster-corrected). The

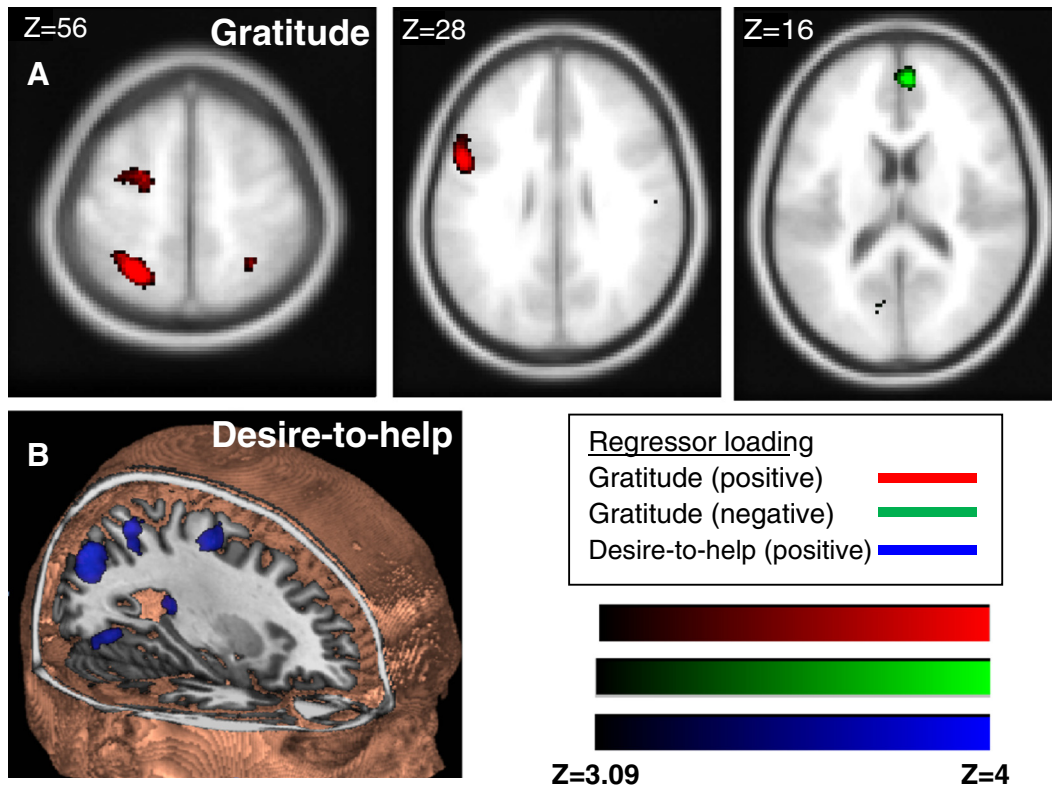


Fig. 2. Neural correlates of motivations during decision-making. (A) Gratitude related neural activity. A regressor at the time of decision-making is parametrically modulated by self-reported gratitude for each trial. The regressor is mean-centered. Regions in red represent areas that showed a significant positive loading on the gratitude rating regressor across the population of all subjects. Regions in green show negative loading. Shown at an uncorrected threshold of $p < 0.001$ for visualization purposes. Significant clusters are shown in Table 2. (B) Desire-to-help related neural activity. As in Fig. 2A, except that the parametrically-modulated regressors track the self-reported desire to help the beneficiary on each trial.

Table 2

Gratitude-related activation. Regions that load on the gratitude parametric modulator at the time of decision making. Clusters defined at an uncorrected threshold of $p < 0.001$ (positive modulation) or $p < 0.005$ (negative modulation). The “Cluster P” shows the cluster-corrected probability of the cluster.

Positive modulation	Cluster P	Cluster size	MNI (x, y, z)	Area
	0.001	596	−26, −58, 54	BA7, left superior parietal lobule
	0.002	332	−24, −6, 60	BA6, left superior frontal gyrus
	0.003	307	−52, 8, 26	BA9, left inferior frontal gyrus
	0.023	196	38, −82, −14	BA18, right middle occipital gyrus
Negative modulation	0.013	513	6, 52, 16	BA10, right medial frontal gyrus
	0.048	390	60, −48, 32	BA40, right supramarginal gyrus
	<0.001	1032	−10, −84, 28	BA19, left visual cortex

peak voxels in BA6 and BA9 listed in Table 2 remained significant ($p < 0.001$, uncorrected), and the region in BA18 was not significant.

In the “help-then-gratitude” GLM, we entered the desire-to-help regressor first, and then gratitude (followed by guilt, then percent given). In this GLM, the gratitude effect remained significant in a cluster of 60 voxels in the superior parietal lobule region identified earlier (peak MNI −26, −58, 56, $p < 0.001$, uncorrected), however the cluster as a whole did not pass cluster correction. No other regions showed a significant effect. This confirms that gratitude-related activation shares variance with a desire to help, but neither desire to help nor guilt can completely account for neural activity that correlates with gratitude.

We hypothesized that neural activity related to gratitude in the gratitude task would correlate positively with trait measures of gratitude, in particular the GQ and the GAC3 (McCullough et al., 2002). To test this, we collapsed across both intervention groups and tested for a correlation between the GQ and GAC3 self-report measures and each of the four PM regressors of gratitude, guilt, desire to help, and percent of endowment given. We found no correlations between self-reported gratitude and the parametrically modulated regressors for gratitude or guilt. We did find positive correlations between the GQ and the desire-to-help regressor in the bilateral supplementary motor area (MNI 6, −12, 62; $p < 0.001$, cluster corrected), which is activated with willful actions (Debaere et al., 2003). A scatter plot of this region showed that the result was strongly driven by an outlier (Fig. 3). To investigate this further, we recomputed the correlation without the outlier and found that the correlation was still significant and positive (r -squared = 0.154, $t(40) = 2.70$, $p = 0.01$). We also found positive correlations between the GAC3 and the percent given parametric modulator in the medial prefrontal cortex (MNI −6, 42, 30, $p < 0.001$, cluster corrected), as shown in Fig. 3. No other regions correlated with the trait gratitude measures.

Effect of gratitude intervention

We hypothesized that the gratitude writing intervention would lead to measurable changes in brain activity, and specifically in greater neural activity related to the expression of gratitude. We thus explored the GLM beta weights for the gratitude PM regressor at the time of decision making. We compared these beta weights voxel-by-voxel in those that received the gratitude writing intervention relative to those that received only psychotherapy. Using a between-groups random effects t -test, we found that relative to the therapy-as-usual control group, the gratitude-writing group showed greater loading on the

gratitude PM regressor in a single region, the perigenual anterior cingulate cortex ($p < 0.05$, cluster corrected, MNI −10, 38, 2), as shown in Fig. 4. This dovetails with our finding above that the gratitude writing intervention led to significantly greater self-reported gratefulness in the two weeks following the intervention relative to the therapy-as-usual control group. Also, there was significantly greater loading on the percent-given PM regressor in the gratitude intervention group relative to the therapy-as-usual control group, in the right thalamus at MNI 10, −28, 0 ($p < 0.05$, cluster corrected). There was no between-group effect of the intervention on the guilt PM regressor, nor on the desire-to-help PM regressor. These results are consistent with an effect of neural plasticity, but given that we did not collect baseline functional scans on subjects prior to the gratitude writing intervention, we cannot definitively rule out a pre-existing group difference. This is less likely though given that our subjects were randomized to the three intervention groups, and there were no age, gender, or initial symptom differences between the groups.

Discussion

Until now, very few studies have attempted to determine the neural correlates of gratitude. Structural imaging studies have shown relationships between cortical volume, especially larger right inferior temporal cortical volume, and gratitude traits (Zahn et al., 2014). An earlier study showed that individuals who identify gratitude in a social narrative more often showed greater hypothalamic activity while reading sentences that describe a social interaction (Zahn et al., 2009). This may reflect significant physiological effects of recognizing gratitude. Our findings (Fig. 2) show that greater gratitude expression generally correlated more with activity in parietal and lateral prefrontal cortex rather than with activity in the limbic regions. We found activity correlating with gratitude specifically extending across the intraparietal sulcus and inferior frontal gyrus, both of which have previously been implicated in mental arithmetic specifically (Dehaene et al., 2004; Simon et al., 2002). This is consistent with the nature of our task, which required subjects to operationalize and quantify their gratitude as a payment amount. A very recent paper also shows a correlation between self-reported gratitude experience and pre-genual medial prefrontal cortex activity (Fox et al., 2015), in a region that appears to overlap with the region showing between-groups effect of the gratitude intervention in our study (Fig. 4). This provides converging evidence for this region's role in gratitude-related cognitive processes.

Gratitude consists of both experience and expression, and our task also required a reflective self-report of gratitude experience after each gratitude expression. For our GLM analysis, we chose to model the gratitude-related neural activity at the time when gratitude was expressed, i.e. when they chose how much money to pay forward. An alternative possibility would be to model gratitude earlier, at the time when the initial endowment was received and gratitude may have been experienced, or later when subjects self-report their degree of gratitude motivation. Our analysis reflects a construction of gratitude as an expression rather than an experience *per se*. Put another way, gratitude has prosocial effects by virtue of its expression — if one experiences positive affect as a consequence of receiving benefit, the

Table 3

Desire to help effects. Regions that load on the desire-to-help parametric modulator at the time of decision making. Clusters defined at an initial uncorrected threshold of $p < 0.001$, and the “Cluster P” shows the cluster-corrected probability of the cluster.

Cluster P	Cluster size	MNI (x, y, z)	Area
0.001	404	−30, −80, 36	Left mid-occipital
0.004	232	−30, −12, 58	BA6, left precentral gyrus
0.001	279	−30, −56, 58	BA7, left superior parietal lobule
0.025	157	−20, −74, −18	Left cerebellar declive

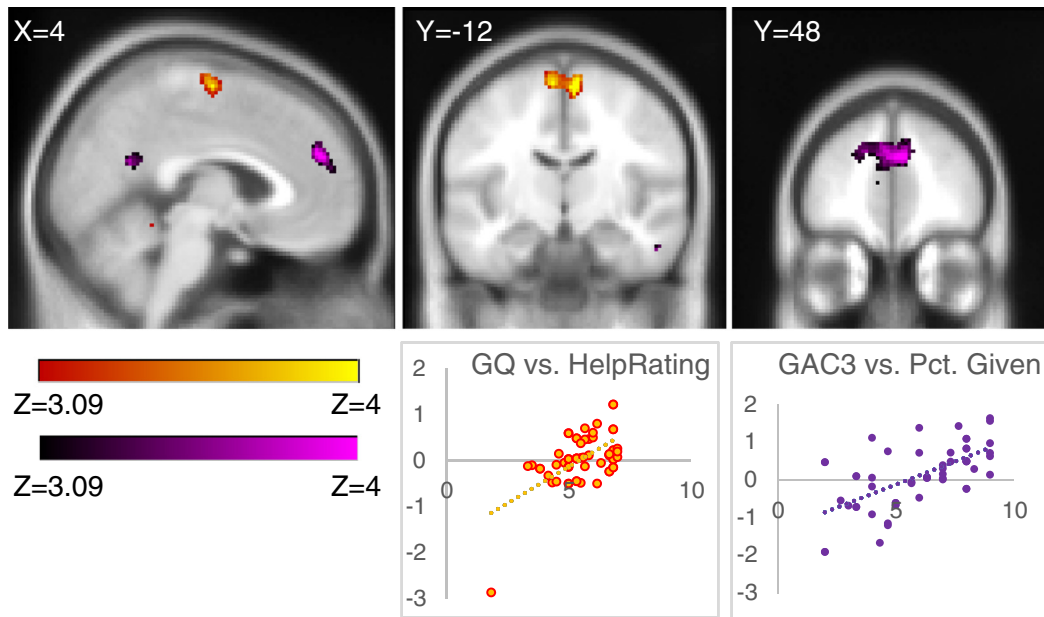


Fig. 3. Neural correlates of trait gratitude measures. The region in orange shows a significant correlation across all subjects between the GQ self-report measure (McCullough et al., 2002) and the GLM regressor that is parametrically modulated by the desire to help (peak MNI = 6, -12, 62, $p < 0.001$ cluster corrected, 399 voxels. Peak voxel $Z = 4.40$). The corresponding scatterplot is shown in orange. The correlation in this region remains significant even when excluding the outlier (r -squared = 0.154, $p = 0.01$). The medial prefrontal region in violet shows a significant correlation across all subjects between the GAC3 self report measure (McCullough et al., 2002) and the GLM regressor that is parametrically modulated by the percent of the initial endowment given (peak MNI = -6, 42, 30, $p < 0.001$, cluster corrected, 622 voxels. Peak voxel $Z = 4.38$). The corresponding scatterplot is shown in violet. All contrasts are visualized at $p < 0.001$ uncorrected.

experience has no direct prosocial value unless it is converted into an expression of gratitude. It is the activity during the expression of gratitude that we measure here. Of note, subjects also evaluated and self-reported their experience of gratitude in deciding how much money to give, but that self-report happened later in each trial. Our neuroimaging analyses thus modeled neural activity at the time when subjects decided how much to give, and the regressors were parametrically modulated by the subsequently self-reported gratitude, desire-to-help, and guilt motivation values in each trial.

It is also noteworthy that our “Pay It Forward” task involves gratitude expressed as monetary gifting to a third party. This differs somewhat from a more typical expression of gratitude as reciprocal, in that gratitude is expressed to the person one is grateful to. We believe this approach is justified on the basis that the benefactor specifically requests that gratitude be expressed this way, and also many subjects did report experiencing substantial gratitude as a motivating factor in their task decisions, as measured by the self-report during the task.

Still, our analysis subtly assumes that subjects modulated their donation amount in proportion to how grateful they felt, per the instructions, such that the donation amount was directly driven by the felt gratitude. This assumption would be violated to the extent that subjects were not intrinsically motivated to donate more out of gratitude, but instead were simply attempting to comply with the experimenter instructions. Nevertheless, in either case, the regions where activity correlates with self-reported gratitude ratings may reflect an operationalized expression of gratitude.

Besides gratitude experience vs. expression vs. evaluation, the motor effects of button pressing present a potential confound, so we carefully counterbalanced the subjects to control motor confounds and included separate motor regressors as nuisance covariates. We counterbalanced across subjects the motor (button press) mappings to different levels of gratitude expression (operationalized as monetary gifts), so neural activity related to gratitude expression is not confounded with simple motor activity here.

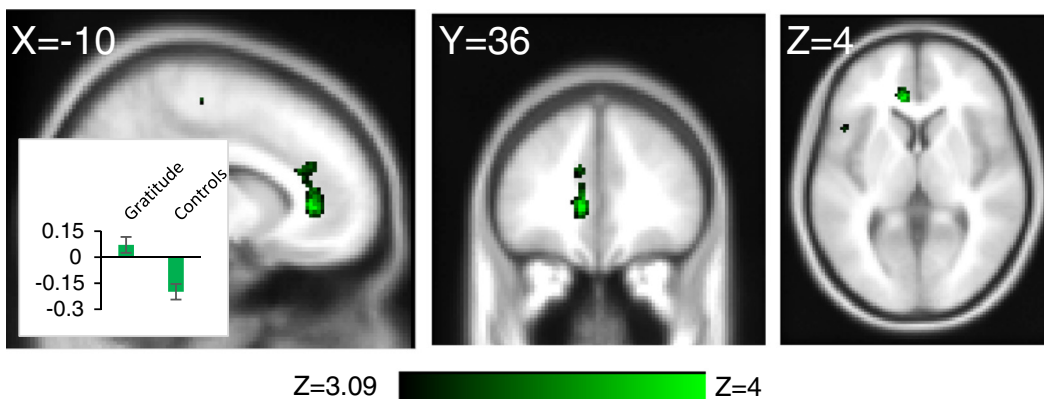


Fig. 4. Effects of prior gratitude intervention on brain activity three months post-treatment. The contrast shows the greater loading of the gratitude rating parametrically modulated regressor on the gratitude intervention group relative to the control group. The pregenual anterior cingulate cluster shown (Peak MNI = -10, 38, 2) is significant at the level of the cluster, $p < 0.05$. Inset: The gratitude PM regressor loads positively on the region in the gratitude group (arbitrary units), but it loads negatively in the therapy-as-usual control group.

Tables 2 and 3 summarize the brain regions that are modulated by self-reported gratitude and desire to help. It is essential to recall that the activities are measured at the time when a decision is made regarding how much to give, and not at the time later when motivations are reported. We find that a number of regions in the frontal, parietal, and occipital lobes show greater activity when gratitude motivations are greater. Some regions notably show activity that is decreased when gratitude motivation is greater.

We also explored whether gratitude involves brain regions related to social and affective processes, and we found some evidence in support of this hypothesis. Gratitude may involve positive affect and a focus on other people rather than self. In that sense, it is perhaps most related to empathy, which may be either positively or negatively valenced, and that is other-oriented as well (Tangney et al., 2007). The neurobiology of empathy has been studied thoroughly and generally involves the anterior cingulate cortex and anterior insula (Singer et al., 2004, 2009), as well as the amygdala and *pars opercularis* in the inferior frontal gyrus (IFG) (Bzdok et al., 2012; Carr et al., 2003; Moll et al., 2002; Shamay-Tsoory et al., 2009). The region we found that loaded on the gratitude parametric modulated regressor (Fig. 2A) was found in BA9, which was distinct from earlier reports of empathy effects in the *pars opercularis* BA44. Nevertheless, our between-groups finding of greater activity in the pregenual anterior cingulate cortex are consistent with recent reports (Fox et al., 2015), which may be consistent with empathy, theory of mind, and moral cognition-related activation.

The constructs of cognitive mentalizing and theory of mind (ToM) are closely related and have been found to involve overlapping brain regions (Bzdok et al., 2012), though they were found to be distinct in that they are connected with different networks (Vollm et al., 2006). Cognitive mentalizing and ToM operations involve overlapping activations in the medial prefrontal cortex, superior temporoparietal junction (TPJ), and temporal poles, however the ToM also includes activations in the frontal gyrus, cuneus, and superior temporal gyrus (Vollm et al., 2006). Notably, there are no common regions of brain activation involved in cognitive mentalizing that overlap with regions found to be activated in the present study. Other than the activation in the IFG, significant activations were found in the left superior parietal lobule, left superior frontal gyrus, and the right middle occipital gyrus, all of which are not within the same regions as common literature observing the cognitive mentalizing system. Still, our results show activation related to gratitude and the desire to help (Fig. 2B) in the left superior parietal lobule (BA7). This region is at least adjacent to the TPJ, which is involved in ToM (Saxe and Kanwisher, 2003), among other functions (Mitchell, 2008). Overall, a recent meta-analysis has identified regions associated with ToM, empathy, and moral cognition (Bzdok et al., 2012), but we find little if any overlap between the regions identified by the meta-analysis and the regions showing significant effects of gratitude here.

It was particularly noteworthy that the gratitude intervention was associated with such a lasting increase in pregenual anterior cingulate responsiveness to gratitude, even three months later (Fig. 4). The intervention lasted around an hour in all, which is relatively short given the lasting nature of the effects. This finding may reflect a neural plasticity effect, but it must also be treated with caution. This was a cross-sectional study. The subjects were randomized into groups, and there were no significant differences in the age, gender, trait gratitude (GQ) or clinical symptom scores between groups. A significant constraint on interpreting our results stems from the fact that we did not perform initial fMRI scans pre-intervention due to budget constraints. Thus, we cannot definitively rule out a possible pre-existing between-group difference in neural sensitivity to gratitude, despite the absence of pre-existing differences in trait gratitude. The pre-intervention scans would be necessary to conclude that there is a neural plasticity effect, and a follow-up study would be warranted by these results. Also, the therapy-as-usual control group can be considered a passive control, as we simply omitted the gratitude writing intervention. This means that

part of the group differences could be due to the writing itself, apart from the specific content of the writing. We considered using the expressive writing condition as an active control group, but given the absence of similar previous studies, we elected to cast a wide net and leave the further dissection of gratitude writing effects to future studies.

The particular region showing between-groups effects in Fig. 4 overlaps with another region very recently reported as correlating with gratitude (Fox et al., 2015). It also overlaps with a similar region found to be altered by mindfulness interventions (Allen et al., 2012), which have also been shown to increase gratitude (Shapiro et al., 2002). Functionally, the pregenual anterior cingulate has been shown to be involved in predicting the outcomes of actions (Alexander and Brown, 2011; Jahn et al., 2014) and in dual task performance (Dreher, 2003). This suggests a possible mechanistic account of the gratitude intervention: specifically, it may increase the neural activity related to predicting the effects of one's actions on another person. To the extent one predicts and evaluates the likely effects of one's actions on others, one might be more willing to direct those actions towards having a positive impact on others. For example, individuals who role-play typically report greater empathy for the subjects whose roles they are playing (Poorman, 2002).

The measures of trait gratitude (especially the GQ) showed a correlation between gratitude and the activity related to desire to help in the supplementary motor area (SMA), as shown in Fig. 3. The desire to help is conceptually related to altruism, which may also be driven by empathy (De Waal, 2008). In any case, the SMA is generally involved in motor functions and may reflect a greater neural preparation to act as an expression of gratitude. Studies of altruism have generally shown activity in the posterior superior temporal cortex, which has been suggested to be related to prediction of the beliefs of others or their actions in an environment (Saxe and Kanwisher, 2003; Singer et al., 2004; Tankersley et al., 2007; Vollm et al., 2006). Thus, our results suggest that gratitude and the neural underpinnings of a desire to help in the SMA may be distinct from effects related to altruism.

Similarly, trait gratitude (especially the GAC3) showed a correlation with neural activity in the medial prefrontal cortex related to the percent of the endowment given. This region is adjacent to the region that showed lasting effects of the gratitude intervention and may reflect a cognitive process related to predicting the results of one's actions (Jahn et al., 2014).

Our study has a few limitations. First, because the gratitude rating regressor and the desire to help regressor were partially correlated in the GLM, we cannot be sure that the regions showing a correlation with gratitude would not also show some correlation with the desire to help, and *vice versa*. We partially addressed this by entering the guilt and desire to help regressors before gratitude in a follow-up GLM analysis. This essentially partialled out the guilt and desire to help signals in the neural activity, and we found that the gratitude rating regressor loadings remained significant in several of the regions. Still, future studies may be able to decorrelate these factors in the experimental design, but that was not possible with our self-report approach. Second, it is possible that the scanner environment and static pictures of benefactors and beneficiaries may not fully recreate the social experience of interacting with people in a prosocial manner. This is a limitation that confronts all such studies of social interactions to varying degrees. This may partly account for the relative lack of affective brain region activity observed here. Nevertheless, the task was valid in that participants knew that they would get to keep the part of an endowment they chose to keep and that the remaining part would in fact be given to a charitable cause. All subjects did in fact choose to donate part of their endowments and reported experiencing gratitude, which suggests that the task was successful in evoking prosocial experiences and actions.

Another potential limitation of our study is that we recruited from a population seeking counseling for anxiety and/or depression. There was no significant difference between the two groups in terms of the mental health scores either before or after the interventions, but the average

mental health score at intake reflected more anxiety and/or depression than the normal healthy population. For this reason, we cannot rule out the possibility that the effects we observed may differ in a normal healthy population.

Overall, our results suggest a nuanced view of the neural mechanisms of gratitude. It is somewhat distinct at the neural level from empathy, theory of mind, and altruism, despite some modest overlap. It involves neural mechanisms associated with predicting the effects of one's actions, mental arithmetic and calculations, and carrying out multiple tasks at once. We show here that even brief expressions of gratitude may have profound and lasting effects on neural activity and sensitivity, perhaps related to monitoring of self and others, which may have implications for practices and interventions involving gratitude expression.

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References

- Alexander, W.H., Brown, J.W., 2010. Computational models of performance monitoring and cognitive control. *Top. Cogn. Sci.* 2, 658–677.
- Alexander, W.H., Brown, J.W., 2011. Medial prefrontal cortex as an action-outcome predictor. *Nat. Neurosci.* 14, 1338–1344. <http://dx.doi.org/10.1038/nn.2921>.
- Allen, M., Dietz, M., Blair, K.S., van Beek, M., Rees, G., Vestergaard-Poulsen, P., Lutz, A., Roepstorff, A., 2012. Cognitive-affective neural plasticity following active-controlled mindfulness intervention. *J. Neurosci.* <http://dx.doi.org/10.1523/JNEUROSCI.2957-12.2012>.
- Baxter, H.J., Johnson, M.H., Bean, D., 2012. Efficacy of a character strengths and gratitude intervention for people with chronic back pain. *Aust. J. Rehabil. Couns.* 18, 135–147. <http://dx.doi.org/10.1017/jrc.2012.14>.
- Berg, J., Dickhaut, J., McCabe, K., 1995. Trust, reciprocity, and social history. *Games Econ. Behav.* 10, 122–142.
- Boehm, J.K., Lyubomirsky, S., Sheldon, K.M., 2011. A longitudinal experimental study comparing the effectiveness of happiness-enhancing strategies in Anglo Americans and Asian Americans. *Cogn. Emot.* <http://dx.doi.org/10.1080/02699931.2010.541227>.
- Brown, J.W., Braver, T.S., 2007. Risk prediction and aversion by anterior cingulate cortex. *Cogn. Affect. Behav. Neurosci.* 7, 266–277.
- Bzdok, D., Schilbach, L., Vogeley, K., Schneider, K., Laird, A.R., Langner, R., Eickhoff, S.B., 2012. Parsing the neural correlates of moral cognition: ALE meta-analysis on morality, theory of mind, and empathy. *Brain Struct. Funct.* 217, 783–796. <http://dx.doi.org/10.1007/s00429-012-0380-y>.
- Carr, L., Iacoboni, M., Dubeau, M.-C., Mazziotta, J.C., Lenzi, G.L., 2003. Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proc. Natl. Acad. Sci. U. S. A.* 100, 5497–5502. <http://dx.doi.org/10.1073/pnas.0935845100>.
- Cheng, S.-T., Tsui, P.K., Lam, J.H.M., 2015. Improving mental health in health care practitioners: randomized controlled trial of a gratitude intervention. *J. Consult. Clin. Psychol.* 83, 177–186. <http://dx.doi.org/10.1037/a0037895>.
- Chiu, P.H., Kayali, M.A., Kishida, K.T., Tomlin, D., Klinger, L.G., Klinger, M.R., Montague, P.R., 2008. Self responses along cingulate cortex reveal quantitative neural phenotype for high-functioning autism. *Neuron* 57, 463–473. <http://dx.doi.org/10.1016/j.neuron.2007.12.020>.
- Coricelli, G., Critchley, H., Joffily, M., O'Doherty, J., Sirigu, A., Dolan, R.J., 2005. Regret and its avoidance: a neuroimaging study of choice behavior. *Nat. Neurosci.* 8, 1255–1262.
- De Quervain, D.J.-F., Fischbacher, U., Treyer, V., Schellhammer, M., Schnyder, U., Buck, A., Fehr, E., 2004. The neural basis of altruistic punishment. *Science* 305, 1254–1258. <http://dx.doi.org/10.1126/science.1100735>.
- De Waal, F.B.M., 2008. Putting the altruism back into altruism: the evolution of empathy. *Annu. Rev. Psychol.* 59, 279–300. <http://dx.doi.org/10.1146/annurev.psych.59.103006.093625>.
- Debaere, F., Wenderoth, N., Sunaert, S., Van Hecke, P., Swinnen, S.P., 2003. Internal vs external generation of movements: differential neural pathways involved in bimanual coordination performed in the presence or absence of augmented visual feedback. *NeuroImage* 19, 764–776. [http://dx.doi.org/10.1016/S1053-8119\(03\)00148-4](http://dx.doi.org/10.1016/S1053-8119(03)00148-4).
- Dehaene, S., Molko, N., Cohen, L., Wilson, A.J., 2004. Arithmetic and the brain. *Curr. Opin. Neurobiol.* <http://dx.doi.org/10.1016/j.conb.2004.03.008>.
- Deichmann, R., Gottfried, J.A., Hutton, C., Turner, R., 2003. Optimized EPI for fMRI studies of the orbitofrontal cortex. *NeuroImage* 19, 430–441.
- Dreher, J.-C., 2003. Dissociating the roles of the rostral anterior cingulate and the lateral prefrontal cortices in performing two tasks simultaneously or successively. *Cereb. Cortex* 13, 329–339. <http://dx.doi.org/10.1093/cercor/13.4.329>.
- Emmons, R.A., McCullough, M.E., 2003. Counting blessings versus burdens: an experimental investigation of gratitude and subjective well-being in daily life. *J. Pers. Soc. Psychol.* <http://dx.doi.org/10.1037/0022-3514.84.2.377>.
- Emmons, R.A., Mishra, A., 2012. Why gratitude enhances well-being: what we know, what we need to know. In: Kashdan, T., Steger, M.F. (Eds.), *Designing the Future of Positive Psychology: Taking Stock and Moving Forward*. Oxford University Press, New York.
- Emmons, R.A., Stern, R., 2013. Gratitude as a psychotherapeutic intervention. *J. Clin. Psychol.* 69, 846–855. <http://dx.doi.org/10.1002/jclp.22020>.
- Flinchbaugh, C.L., Moore, E.W.G., Chang, Y.K., May, D.R., 2012. Student well-being interventions: the effects of stress management techniques and gratitude journaling in the management education classroom. *J. Manag. Educ.* 36, 191–219. <http://dx.doi.org/10.1177/1052562911430062>.
- Fox, G.R., Kaplan, J., Damasio, H., Damasio, A., 2015. Neural correlates of gratitude. *Front. Psychol.* 6. <http://dx.doi.org/10.3389/fpsyg.2015.01491>.
- Friston, K.J., Williams, S., Howard, R., Frackowiak, R.S.J., Turner, R., 1996. Movement-related effects in fMRI time-series. *Magn. Reson. Med.* 35, 346–355.
- Froh, J.J., Sefick, W.J., Emmons, R.A., 2008. Counting blessings in early adolescents: an experimental study of gratitude and subjective well-being. *J. Sch. Psychol.* 46, 213–233. <http://dx.doi.org/10.1016/j.jsp.2007.03.005>.
- Fukunaga, R., Brown, J.W., Bogg, T., 2012. Decision making in the Balloon Analogue Risk Task (BART): anterior cingulate cortex signals loss aversion but not the infrequency of risky choices. *Cogn. Affect. Behav. Neurosci.* 12, 479–490. <http://dx.doi.org/10.3758/s13415-012-0102-1>.
- Geraghty, A.W.A., Wood, A.M., Hyland, M.E., 2010. Dissociating the facets of hope: agency and pathways predict dropout from unguided self-help therapy in opposite directions. *J. Res. Pers.* 44, 155–158. <http://dx.doi.org/10.1016/j.jrp.2009.12.003>.
- Harris, L.T., McClure, S.M., van den Bos, W., Cohen, J.D., Fiske, S.T., 2007. Regions of the MPFC differentially tuned to social and nonsocial affective evaluation. *Cogn. Affect. Behav. Neurosci.* 7, 309–316. <http://dx.doi.org/10.3758/CABN.7.4.309>.
- Jahn, A., Nee, D.E., Alexander, W.H., Brown, J.W., 2014. Distinct regions of anterior cingulate cortex signal prediction and outcome evaluation. *NeuroImage* 95, 80–89. <http://dx.doi.org/10.1016/j.neuroimage.2014.03.050>.
- Johnstone, T., Ores Walsh, K.S., Greischar, L.L., Alexander, A.L., Fox, A.S., Davidson, R.J., Oakes, T.R., 2006. Motion correction and the use of motion covariates in multiple-subject fMRI analysis. *Hum. Brain Mapp.* 27, 779–788. <http://dx.doi.org/10.1002/hbm.20219>.
- Kaczmarek, L.D., Kashdan, T.B., Drajkowski, D., Enko, J., Kosakowski, M., Szäfer, A., Bujacz, A., 2015. Why do people prefer gratitude journaling over gratitude letters? The influence of individual differences in motivation and personality on web-based interventions. *Personal. Individ. Differ.* 75, 1–6. <http://dx.doi.org/10.1016/j.paid.2014.11.004>.
- Kerr, S.L., O'Donovan, A., Pepping, C.A., 2015. Can gratitude and kindness interventions enhance well-being in a clinical sample? *J. Happiness Stud.* 16, 17–36. <http://dx.doi.org/10.1007/s10902-013-9492-1>.
- Killen, A., Macaskill, A., 2015. Using a gratitude intervention to enhance well-being in older adults. *J. Happiness Stud.* 16, 947–964. <http://dx.doi.org/10.1007/s10902-014-9542-3>.
- King-Casas, B., Tomlin, D., Anen, C., Camerer, C.F., Quartz, S.R., Montague, P.R., 2005. Getting to know you: reputation and trust in a two-person economic exchange. *Science* 308, 78–83. <http://dx.doi.org/10.1126/science.1108062> (80-, doi:308/5718/78 [pii]).
- Kopta, S.M., Lowry, J.L., 2002. Psychometric evaluation of the behavioral health questionnaire-20: a brief instrument for assessing global mental health and the three phases of psychotherapy outcome. *Psychother. Res.* 12, 413–426. <http://dx.doi.org/10.1093/ptr/12.4.413>.
- Layous, K., Chancellor, J., Lyubomirsky, S., Wang, L., Doraiswamy, P.M., 2011. Delivering happiness: translating positive psychology intervention research for treating major and minor depressive disorders. *J. Altern. Complement. Med.* 17 (8), 675–683. <http://dx.doi.org/10.1089/acm.2011.0139>.
- Lyubomirsky, S., Dickerhoof, R., Boehm, J.K., Sheldon, K.M., 2011. Becoming happier takes both a will and a proper way: an experimental longitudinal intervention to boost well-being. *Emotion* 11, 391–402. <http://dx.doi.org/10.1037/a0022575>.
- McCullough, M.E., Kilpatrick, S.D., Emmons, R.A., Larson, D.B., 2001. Is gratitude a moral affect? *Psychol. Bull.* 127, 249–266. <http://dx.doi.org/10.1037/0033-2909.127.2.249>.
- McCullough, M.E., Emmons, R.A., Tsang, J.-A., 2002. The grateful disposition: a conceptual and empirical topography. *J. Pers. Soc. Psychol.* 82, 112–127. <http://dx.doi.org/10.1037/0022-3514.82.1.112>.
- Mitchell, J.P., 2008. Activity in right temporo-parietal junction is not selective for theory-of-mind. *Cereb. Cortex* 18, 262–271. <http://dx.doi.org/10.1093/cercor/bhm051>.
- Moll, J., de Oliveira-Souza, R., Eslinger, P.J., Bramati, I.E., Mourão-Miranda, J., Andreiulo, P.A., Pessoa, L., 2002. The neural correlates of moral sensitivity: a functional magnetic resonance imaging investigation of basic and moral emotions. *J. Neurosci.* (doi:20026214).
- O'Leary, K., Dockray, S., 2015. The effects of two novel gratitude and mindfulness interventions on well-being. *J. Altern. Complement. Med.* 21, 243–245. <http://dx.doi.org/10.1089/acm.2014.0119>.
- Oppenheim, A.V., Shafer, R.W., Buck, J.R., 1999. *Discrete Time-Signal Processing*. Prentice Hall, Upper Saddle River, NJ.
- Poorman, P.B., 2002. Biography and role playing: foster empathy in abnormal psychology. *Teach. Psychol.* 29, 32–36. http://dx.doi.org/10.1207/S15328023TOP2901_08.
- Rameson, L.T., Morelli, S.A., Lieberman, M.D., 2012. The neural correlates of empathy: experience, automaticity, and prosocial behavior. *J. Cogn. Neurosci.* 24, 235–245. <http://dx.doi.org/10.1162/jocn.2010.00130>.
- Sanfey, A.G., Rilling, J.K., Aronson, J.A., Nystrom, L.E., Cohen, J.D., 2003. The neural basis of economic decision-making in the ultimatum game. *Science* 300, 1755–1758 (80-).
- Saxe, R., Kanwisher, N., 2003. People thinking about thinking people: the role of the temporo-parietal junction in "theory of mind." *NeuroImage* 19, 1835–1842. [http://dx.doi.org/10.1016/S1053-8119\(03\)00230-1](http://dx.doi.org/10.1016/S1053-8119(03)00230-1).

- Seligman, M.E.P., Steen, T.A., Park, N., Peterson, C., 2005. Positive psychology progress. *Am. Psychol.* 60, 410–421. <http://dx.doi.org/10.1037/0003-066X.60.5.410>.
- Shamay-Tsoory, S.G., Aharon-Peretz, J., Perry, D., 2009. Two systems for empathy: a double dissociation between emotional and cognitive empathy in inferior frontal gyrus versus ventromedial prefrontal lesions. *Brain* 132, 617–627. <http://dx.doi.org/10.1093/brain/awn279>.
- Shapiro, S.L., Schwartz, G.E.R., Santerre, C., Shapiro, S.L., Gary Schwartz, C.S., 2002. *Meditation and positive psychology*. *Handbook of Positive Psychology*, pp. 632–645.
- Sheldon, K.M., Lyubomirsky, S., 2006. How to increase and sustain positive emotion: the effects of expressing gratitude and visualizing best possible selves. *J. Posit. Psychol.* <http://dx.doi.org/10.1080/17439760500510676>.
- Simon, O., Mangin, J.F., Cohen, L., Le Bihan, D., Dehaene, S., 2002. Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. *Neuron* 33, 475–487. [http://dx.doi.org/10.1016/S0896-6273\(02\)00575-5](http://dx.doi.org/10.1016/S0896-6273(02)00575-5).
- Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R.J., Frith, C.D., 2004. Empathy for pain involves the affective but not sensory components of pain. *Science* 303, 1157–1162. <http://dx.doi.org/10.1126/science.1093535> 303/5661/1157 (80–, pii).
- Singer, T., Seymour, B., O'Doherty, J.P., Stephan, K.E., Dolan, R.J., Frith, C.D., 2006. Empathic neural responses are modulated by the perceived fairness of others. *Nature* 439, 466–469. <http://dx.doi.org/10.1038/nature04271>.
- Singer, T., Critchley, H.D., Preuschoff, K., 2009. A common role of insula in feelings, empathy and uncertainty. *Trends Cogn. Sci.* 13, 334–340. <http://dx.doi.org/10.1016/j.tics.2009.05.001> (doi:S1364-6613(09)00135-1 [pii]).
- Tangney, J.P., Stuewig, J., Mashek, D.J., 2007. Moral emotions and moral behavior. *Annu. Rev. Psychol.* 58, 345–372. <http://dx.doi.org/10.1146/annurev.psych.56.091103.070145>.
- Tankersley, D., Stowe, C.J., Huettel, S.A., 2007. Altruism is associated with an increased neural response to agency. *Nat. Neurosci.* 10, 150–151. <http://dx.doi.org/10.1038/nn1833>.
- Tomlin, D., Kayali, M.A., King-Casas, B., Anen, C., Camerer, C.F., Quartz, S.R., Montague, P.R., 2006. Agent-specific responses in the cingulate cortex during economic exchanges. *Science* 312, 1047–1050. <http://dx.doi.org/10.1126/science.1125596>.
- Vollm, B.A., Taylor, A.N., Richardson, P., Corcoran, R., Stirling, J., McKie, S., Deakin, J.F., Elliott, R., 2006. Neuronal correlates of theory of mind and empathy: a functional magnetic resonance imaging study in a nonverbal task. *NeuroImage* 29, 90–98 (doi:S1053-8119(05)00511-2 [pii]|r10.1016/j.neuroimage.2005.07.022).
- Watkins, P.C., Woodward, K., Stone, T., Kolts, R.L., 2003. Gratitude and happiness: development of a measure of gratitude, and relationships with subjective well-being. *Soc. Behav. Personal. Int. J.* <http://dx.doi.org/10.2224/sbp.2003.31.5.431>.
- Wong, J., Owen, J., Gabana, N., Brown, J., McInnis, S., Toth, P., Gilman, L., n.d. Does gratitude writing improve the mental health of psychotherapy clients? Evidence from a Randomized Controlled Study.
- Wood, A.M., Maltby, J., Stewart, N., Linley, P.A., Joseph, S., 2008. A social-cognitive model of trait and state levels of gratitude. *Emotion* 8, 281–290. <http://dx.doi.org/10.1037/1528-3542.8.2.281>.
- Zahn, R., Moll, J., Paiva, M., Garrido, G., Krueger, F., Huey, E.D., Grafman, J., 2009. The neural basis of human social values: evidence from functional MRI. *Cereb. Cortex* 19, 276–283. <http://dx.doi.org/10.1093/cercor/bhn080>.
- Zahn, R., Garrido, G., Moll, J., Grafman, J., 2014. Individual differences in posterior cortical volume correlate with proneness to pride and gratitude. *Soc. Cogn. Affect. Neurosci.* 9, 1676–1683. <http://dx.doi.org/10.1093/scan/nst158>.